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VOL. 102.

1951.

1 OBSERVATIONS ON THE SOCIAL WASPS OF SOUTH AMERICA (HYMENOPTERA VESPIDAE)

By O. W. and M. J. RICHARDS.

Manuscript received 5th October, 1949.

(Read 3rd May, 1950.)

With 4 Plates and 25 Text-figures.

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1. GENERAL INTRODUCTION.

IN 1937, with the aid of a grant from the Leverhulme Trustees, we spent about two months in British Guiana, principally studying the biology of social wasps. We were accompanied by Dr. J. Smart (British Museum, Natural History), Miss J. Smart, and Mr. N. Y. Sandwith (Royal Botanic Gardens, Kew). Both directly from Dr. Smart, and through him from the authorities of the British Museum, we received invaluable help. Mr. Sandwith's wide knowledge of S. American vegetation was freely put at our disposal in a way which was greatly appreciated. Through the mediation of the Colonial Office much kind help was given to us by the British Guiana authorities, especially the Dept. of Woods and Forests (Mr. B. S. Wood and Mr. T. A. W. Davis). Most of our time was spent at the Government rest-house, Mazaruni Settlement, but we were also able to spend 10 days on the Kaieteur Savannah, at the head of the falls.

The bulk of all the Aculeate Hymenoptera is being deposited in the British Museum collection as the species are worked out. So far this has been done for *Mischocyttarus* Sauss. (Richards, 1945), and now for the remaining social VESPIDAE. Observations made by the senior author on the Oxford University Expedition to British Guiana, 1929, are also included. A loan of a small collection of VESPIDAE from the British Guiana Dept. Agriculture (= Dept. Agric.) was kindly arranged by Mr. L. D. Cleare, Jr. In the study of the specimens in London much kind help has been received from Mr. R. B. Benson, of the British Museum, and, by correspondence, from Dr. J. Bequaert, of the Museum of Comparative Zoology, Cambridge, Mass. There is, therefore, a considerable number of people whom we are glad to take this opportunity of thanking for help of various kinds. The field work in Guiana was done jointly; all dissections and photography, and some biometrical work were done by M.J.R.; the systematic work and the study of the literature were done by O.W.R.

We should like also to pay here a tribute to the work of our predecessors, especially to the von Iherings, father and son, who laid the foundations of our knowledge of reproduction and castes in S. American social wasps, and to the great Adolfo Ducke whose abilities as a naturalist, collector and taxonomist were alike unrivalled. As Bequaert (1938: 99) has remarked, Ducke's paper (1910) is still the foundation of all work on S. American POLYBIINAE.

2. THE SOCIAL WASPS OF SOUTH AMERICA.

Although the common wasps (VESPINAE) of our countryside do not occur in S. America, that country must be regarded as the metropolis of social wasps, from the variety of genera and the number of species (Ducke, 1910; Bequaert, 1918). The South American wasps belong either to the cosmopolitan genus *Polistes* Latr. (about 36 species), or to the 20 genera of POLYBIINAE (about 190 species). Outside S. America the POLYBIINAE are little developed and are represented by *Polybioides* R. du Buyss. (a few species in Africa and Indo-Malaya), *Belonogaster* Sauss. (about 35 species in Africa, extending to Persia), and *Parapolybia* Sauss. (Indo-Malaya; not clearly separated from the S. American *Stelopolybia* Ducke).

Most of our observations were made on the POLYBIINAE. The species

found in British Guiana have recently been revised by Bequaert (1944) and this has reduced the systematic work in the present paper to a minimum (cf. Appendices 1 and 2). But the opportunity has been taken to publish records from the British Museum collection.

Biologically, the S. American species of *Polistes* are not very different from those of temperate countries, except that colonies are often founded by swarms rather than by single fertilised females. In the Polybiines, on the other hand, not only are colonies founded by swarms, but each nest may contain a large number of fertilised, egg-laying queens, which, unlike our familiar VESPINAE, are hardly or not distinguishable from the workers externally. Although in general terms these facts are well-known, it is surprising how meagre is the documentation of this side of the subject, most statements in the literature being traceable to a very few original sources. The following seem to be all the records of dissections of samples from nests: H. von Ihering (1896). "*Polybia scutellaris* (White) var. *paulista* Iher." Nest of 4900 wasps; 14 dissected included 4 fertilised and 1 unfertilised queen. *P. scutellaris* (White). Two nests, one of 700, one of rather fewer wasps; contained no males, and 1-2 per cent. and 5 per cent. of fertilised females, respectively.

R. von Ihering (1903). New formed nest of *Polybia scutellaris* (White) contained 3074 wasps, no ♂, 34 ♀, 3040 ♀; 12 ♀ were dissected and 2 were found to be fertilised. In Rio Grande do Sul, there are usually 12-14 females in a nest. A nest of *Brachygastra lecheguana* (Latr.) (= *Nectarina mellifica*) contained almost as many ♂ as ♀. The latter mostly had some eggs developed, but were classed as workers owing to the small size of the spermatheca. R. von Ihering (1904). *Polybia tinctipennis* Fox (= *P. ypiranguensis* Iher.). A swarm of 520 wasps dissected; only 4 fertilised females with developed ovaries. *P. ignobilis* (Hal.) (cited as *P. nigra* Sauss., see Bequaert, 1943: 723). 3882 wasps taken, included 47 ♀ and 11 ♂; 12 ♀ dissected had all been fertilised. R. du Buysson (1905). In a colony of *Brachygastra* (= *Nectarina*) *lecheguana* (Latr.) from Mexico, about one-sixth were females with large free eggs in the oviduct. The really quantitative data seem therefore to be confined to 8 nests belonging to two genera. In most cases the females were picked out by their appearance (abdomen swollen after oviposition), and a few were dissected. Roubaud's (1916) observations on *Belonogaster* and *Ropalidia* [*Icaria*] in Africa make it probable that in these wasps, too, there are several egg-laying females in each colony. His observation on *Polistes marginalis* Fab. may well bear a different interpretation (see Appendix 3). The question is more complicated than these pioneer observers supposed owing to the presence, in many nests, of individuals we have termed intermediates (p. 16). These are unfertilised but have more or less developed ovaries. They may sometimes be young queens but they are not so usually. Unless a large sample of wasps is dissected, or unless the spermatheca is examined in every case for sperm, it is easy to miss the relatively rare queens, and to misidentify some of the intermediates as queens.

This small body of evidence has, of course, been supplemented by the observation that definite workers cannot as a rule be separated externally from the queens, and it has therefore been assumed that many or all of the wasps in the nest might lay eggs.

The evidence as to swarming is much more extensive. Swarms have often

been seen and, as noted by R. von Ihering (1903), a nest of some size may be built before any eggs are laid. The presence of many wasps in a nest, none of whose cells is complete or shows the remains of old cocoons, is a proof that the nest has been founded by a swarm. Important descriptions of swarms will be found in H. von Ihering (1896, 1896a), R. von Ihering (1903, 1904), Ducke (1905, 1910), R. du Buysson (1906), Schwarz (1931), Rau (1933) and FitzGerald (1938). It has not been clearly stated that swarms are almost certainly of two kinds, namely the *normal swarms* which are budded off to found new colonies, and *abnormal swarms* formed when a nest is destroyed in any way which allows the adult wasps to escape. The composition of normal swarms and what fraction of the parent population enters into their formation is completely unknown. We suspect that in such species as *Metapolybia cingulata* (Fab.) or *Polybia bistriata* (Fab.) the majority of the original colony enter the swarm, whereas in such species as *Polybia rejecta* (Fab.) or *P. occidentalis* var. *scutellaris* (White), which have large perennial nests, a large part of the population must stay behind. Seasonal swarming (usually in the spring) from permanent mother colonies has been described in *P. occidentalis*, var. *scutellaris* by Bruch (1936), in Argentina; in *Brachygastra lecheguana* (Latr.) by du Buysson (1905), in Mexico; and in *Epipona tatua* (Cuv.) by Lacordaire (1838), surprisingly enough in the equatorial rain forest of Cayenne. It has been maintained (R. von Ihering, 1904) that swarms never contain males; this is probably true, or at least usual in normal swarms, for recently founded colonies do not include males. Ducke (1905) has described a swarm of *Apoica* which contained males, but this may have been an abnormal swarm. The whole subject is in need of further investigation.

We may now define the terms necessary for describing this aspect of wasp-biology.

1. *Pleometrosis* (Wasmann, see Bequaert, 1923). The presence of more than one egg-laying, fertilised female in the same nest. *Haplometrosis*, presence of only one such female. The terms polygamous (monogamous) and polygynous (monogynous) have been used in the past, but, according to the dictionary, both correctly imply that males have several (or one) wives.

2. *Swarming*. Colony founded by a group of insects of which at least one is a fertilised female.¹ *Non-swarming*. Colony founded by a single fertilised female.

3. *Association*. Colony started by one fertilised female who is afterwards joined by others (females or workers); where the later arrivals are queens = secondary pleometrosis of Wasmann. This is recorded in *Polistes* (Rau, 1933: 110-11; Haldemann, 1936; Pardi, 1942; cf. Bequaert, 1923) and *Belonogaster* (Roubaud, 1916). It still needs to be established that the wasps which associate can come from more than one parent colony. It may, sometimes, be no more than a sort of delayed swarming, in which the members of the swarm arrive at different times.

The present state of our knowledge of these phenomena in social wasps (excluding the STENOGASTRINAE) is shown in Table 1, some data from the later pages of the present paper being included.

¹ Zikán (1935: 149) suggests that in *Protopolybia* and *Protonectarina*, near Rio de Janeiro, swarms consist of large individuals only, i.e. presumptive queens. We found no evidence for this in Guiana.

TABLE 1.
Types of colony-foundation in the VESPIDAE.

	Swarming	Association	Non-swarming
Haplometrotic .	Probably common in <i>Polistes</i> * in tropics; ? sometimes in <i>Belonogaster</i> ; individual nests of various Guiana POLYBIINAE	<i>Polistes</i> ,* sometimes in tropics; <i>Belonogaster</i> ?	<i>Vespa</i> s.l.; <i>Polistes</i> ,* normally in temperate climates, sometimes in tropics; <i>Mischocyttarus</i> usually; <i>Belonogaster</i> sometimes.
Pleometrotic .	Most POLYBIINAE; ? <i>Mischocyttarus</i> rarely; ? <i>Belonogaster</i> sometimes; Probably all or most <i>Ropalidia</i>	<i>Polistes</i> * sometimes in temperate and perhaps in tropical climates; ? <i>Belonogaster</i> sometimes; ? some <i>Ropalidia</i> .	

* In spite of all that has been written about *Polistes*, the position in this genus is far from clear. In temperate regions it is certain that most nests are founded by a single, hibernated, fecundated queen. In the tropics it is certain that some nests are founded by a queen accompanied by a small swarm of workers. Where, in temperate climates, colonies are founded by two or three females, one of which usually becomes the principal egg-layer, there seem to be at least six alternatives. There may be several queens (hibernated, fecundated); there may be a queen accompanied by hibernated, presumably unfecundated, intermediates or workers (cf. *P. versicolor* Fab. in S. Brazil, H. von Ihering, 1896a). These various individuals might come from one or from more than one nest. To settle these questions requires extensive dissections and biometrical studies, and possibly the marking of large numbers of wasps in the autumn (compare the discussion, on p. 108, of the various types of females which may be found).

3. NEST ARCHITECTURE.

H. de Saussure (1853-58, Introduction, p. xxxiv-cxxxv), in the introduction to his monograph of the social wasps, proposed a classification of their nests which most subsequent workers have used. Some of his terms are essential for any discussion of wasp-biology and these are defined and illustrated below. De Saussure divided nests into two primary types, but we think that it is better to add a third. Carl (1934) has recorded a fourth, in an Indian species of *Ropalidia*, but more information as to the mode of growth in such nests is needed.

(1) *Phragmocyttarous* nests. (Fig. 1.)

A single comb is attached by a more or less broad stalk to a branch, leaf or rock. An envelope is built round and in contact with the edge of this comb. A small exit-hole is left in the envelope, usually below the centre of the comb. A second comb is added by building cells beneath the lower part of the envelope, and this is enclosed by building out the envelope anew round its edge. Access to upper combs is through a hole in each of the lower ones which represents the exit-hole of an earlier stage of the nest.² There is no evidence that such nests can grow in any way except by the addition of new combs. A few *phragmocyttarous* nests (*P. bistriata* (Fab.)) rarely have more

² Except, possibly, *Polybia bistriata* (Fab.), see p. 54.

than one comb. The shape of a large nest with many combs may be either spherical, cylindrical or irregular (e.g. a truncated cone, broad end downwards) according to the exact method of growth, but it seems unnecessary to use the terms which de Saussure proposed to describe some of them. Nests of this type are found in the Polybiine genera *Brachygastra* Perty (= *Nectarina* Shuck. and Swains.), *Chartergus* Lep., *Epipona* Latr. (= *Tatua* Sauss.), *Polybia* Lep., *Protonectarina* Ducke, and *Synocoides* Ducke. *Ropalidia montana* Carl (ROPALIDIINAE) and some other species of that genus make a type of nest which Carl (1934 : 688) terms *klimakocytтарous*, but much more information as to how such nests grow is required to distinguish them clearly from phragmocytтарous ones.

(2) *Astelocytтарous* nests [new term]. (Fig. 2.)

A single comb is fixed directly to a tree trunk, wall or leaf. A domed envelope arises from, or from near the edge of the comb. The comb can be increased in length (probably in *Metapolybia* by removing and reconstructing part of the envelope) or a new comb may be constructed with the same long axis, and a new but connected envelope (*Synococa*). De Saussure put these amongst the phragmocytтарous nests, but there seems little justification for doing so.

Such nests are found in *Clypearia* Sauss., *Metapolybia* Ducke, and *Synococa* Sauss. (POLYBIINAE).

(3) *Stelocytтарous* nests.

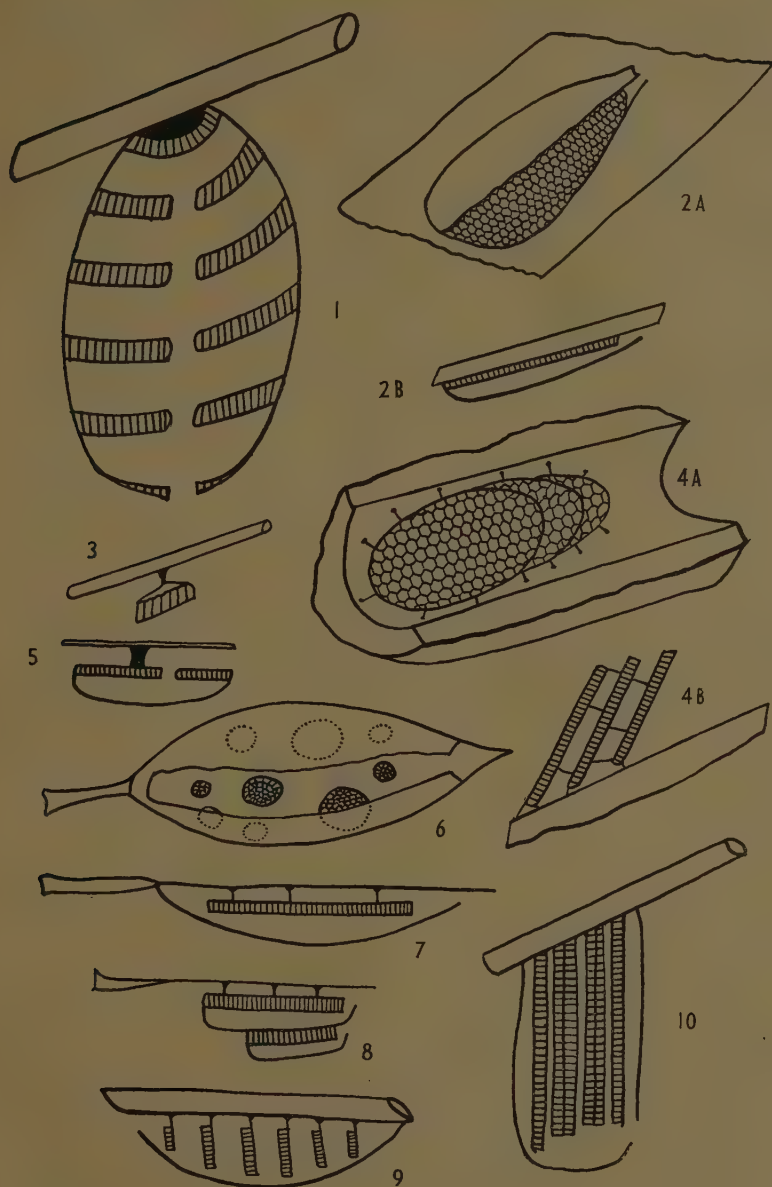
The first comb hangs from the support by one or more pillars. Additional combs, when constructed, are either hung from earlier ones by a pillar, or pillars, or else the combs are fixed to the support side by side, independently. An envelope, if present, is free of the combs (except often the first one in old nests) or attached to them by pillars only. There are therefore no passages through the combs as the wasps crawl between the comb-edges and the envelope. There are three subtypes.

A. *Gymnodomous* nests. No envelope is built.

There is usually only one comb (fig. 3) ; if more than one, the nest is built in a hollow tree or other sheltered place.

EXPLANATION OF FIGURES 1-10.

- FIG. 1. Diagram of a phragmocytтарous nest in section.
 2. Diagram of an astelocytтарous nest ; (a) in surface view, envelope partly removed, (b) in section.
 3. Diagram of gymnodomous, stelocytтарous nest of one comb, in section (*Polistes*, etc.).
 4. Diagram of the same type of nest with several combs in a hollow trunk ; (a) in surface view, (b) in section (*Stelopolybia*).
 5. Diagram of nest of *Charterginus*, in section.
 6. Diagram of nest of *Leipomeles* before the fusion of the combs, surface view, with envelope partly removed.
 7. Diagram of nest of *Leipomeles* after fusion of the combs, in section.
 8. Diagram of nest of *Protopolybia*, in section.
 9. Diagram of nest of *Parachartergus (apicalis)* (Fab., etc.), in section.
 10. Diagram of nest of *Polybioides*, in section.



FIGS. 1-10.

One comb :—POLYBIINAE, *Apoica* Lep.,³ *Belonogaster* Sauss., *Mischocyttarus* Sauss., *Pseudochartergus* Ducke⁴; ROPALIDIINAE, *Ropalidia* Guér. (most species); *Polistes* Latr. (s.l.) (except parasitic species).

Several combs :—POLYBIINAE, *Stelopolybia* Ducke (s.s.) (fig. 4).

B. *Calyptodomous* nests. Combs surrounded by an envelope.

(a) *Rectinidal* nests. Combs more or less parallel to the surface from which they hang; when more than one comb is present, the lower ones hang from the upper ones. POLYBIINAE, *Charterginus* Ducke⁵ (fig. 5), *Leipomeles* Moebius⁶ (figs. 6-7), *Protopolybia* Ducke⁷ (fig. 8), *Pseudopolybia* Sauss.,⁶ *Stelopolybia* Ducke subg. *Angiopolybia* Araujo, *Parapolybia* Sauss.⁸; ROPALIDIINAE, *Ropalidia flavopicta* Sm. (some nests); VESPINAE, all except parasitic species.

(b) *Laterinidal* nests.⁹ Combs at right angles to the surface from which they hang, the petiole being attached to one edge. The combs are parallel to one another and are covered by an envelope which does not touch them. POLYBIINAE, *Parachartergus* R. von Iher. (fig. 9), *Polybioides* R. du Buyss. (fig. 10); ROPALIDIINAE, *Ropalidia flavopicta* (Sm.) (some nests).

There are many minor variations in nest type which will be referred to under the various genera.

Where combs are supported by a single pillar, as in *Mischocyttarus* Sauss., this will be called the *petiole* (Richards, 1945: 301). The cells open on the *distal* surface of the comb, which is normally directed downwards. The back of the comb (the fused bottoms of the cells) is termed the *proximal* surface of the comb. Where the *diameter* of a cell is referred to, it means the shortest distance between any two parallel sides of the hexagon; normally the cell reaches its full diameter when it has reached less than half its length. The *length* of the cells was measured from the centre of the bottom to the rim of the opening. Even in phragmocyttarous nests the cells grow in length with the growth of the larvae. At pupation the cell is lined with a very thin layer of silk and closed by a cocoon-cap which often projects beyond the distal surface of the comb. In some species the workers remove part of the rim of the cell-opening and plaster it in stripes over the cocoon-cap (*Mischocyttarus*

³ The single comb of *Apoica* is really sessile, but it hangs beneath a branch.

⁴ In *Pseudochartergus* the single comb is hidden between leaves to which it is attached by several pillars.

⁵ In *Charterginus* the exit-hole pierces the single comb and opens on the dorsal side of the envelope, between it and the support.

⁶ *Leipomeles* and *Pseudopolybia pusilla* (Ducke) build a group of small petiolated combs under one envelope. The combs ultimately fuse so that the nest becomes rectinidal with several supporting pillars.

⁷ In *Protopolybia* the combs are each in a separate chamber of the envelope, through which there is a separate exit-hole for each story. This arrangement is difficult to make out in the larger nests.

⁸ Schulthess (1927) figures a *Polistes*-like nest in his *Parapolybia meadeana* Schulthess, 1912. According to the type, in the collection of the British Museum, this species actually is a *Polistes*. Dr. J. van der Vecht, however, tells me that some of the Javanese species make a nest of a modified stelocyttarous type, enclosed in an envelope.

⁹ Saussure originally used the term laterinidal for any comb in which the petiole was strongly eccentric, but it is more convenient to restrict its meaning in the present sense. *Polybioides* and *Ropalidia flavopicta* (Sm.) are unique amongst wasps in building cells on both sides of the comb which appears to be sessile.

Richards, 1945 : 302 ; *Polybia dimidiata* (Fab.), *Parachartergus apicalis* (Fab.), R. von Ihering, 1904 : 288 ; *Synoecca surinama* (L.), FitzGerald, 1938 : 189).

There are two quite different types of growth of wasps' nests, depending mainly on whether the species swarms or not. If a single female, or a female and only one or two workers found a colony, cells are constructed relatively slowly, and as the foundations of each one are laid, an egg is placed in it. The number of cells and of eggs (or larvae) increase together at a slow but fairly steady rate. It is unusual to find many empty cells until near the end of the life of the colony, since cells vacated by emerging workers are used again almost at once. This method of growth is seen in *Mischocyttarus*, *Vespa* and most *Polistes*.

On the other hand, where nests are founded by large swarms (*Polybia*, *Parachartergus*, etc.), a nest of some size is built relatively quickly and, at least sometimes, no eggs are laid until this first nest is complete (see R. von Ihering, 1904 : 266, *Polybia fastidiosusula* Sauss. var. *buyssoni* R. von Iher. ; Rau, 1933 : 59, *Polybia occidentalis* (Oliv.)). According to Zikán (1935 : 149), large nests of *Polybia* may be completed in 24 hours. If a series of nests of such a species is examined, it is possible to pick out those which have not increased beyond this initial stage, and it can be shown that there is a characteristic, even if somewhat variable, size for the *initial colony* of each species.

Actually, it appears from analysis of all the nests we examined (p. 112) that the situation is a little more complex. There appear to be in reality three stages in construction : (1) the cells built before any oviposition starts, (2) the cells built by the original swarm before any new workers have emerged, (3) the later additions, largely built by new workers. The distinction between stages 1 and 2 may not be important in all species or colonies ; this point needs investigation. Meanwhile, the term "initial colony" is probably best used for that part of the nest which is built by the original swarm (*i.e.* nests of age less than 1, in the sense of p. 10).

In non-swarving species, the first eggs are laid in the cells adjoining the principal petiole of the comb. In a nest of some size a regular arrangement of developmental stages is found with, perhaps, cocoons near the petiole, followed by larvae of gradually decreasing size, and eggs in the cells furthest from the petiole. As wasps emerge from the cells and these are used again, the regular arrangement is gradually lost. A comb with all stages present, but scattered irregularly, is at once known as one which is considerably older than the length of one life-cycle.

In phragmocytarus nests also there is a similar regular arrangement of the stages in the initial colony or in the recently added combs of older colonies. The first eggs are laid at the centre of the comb, and the contents of these cells are always more mature than those at the periphery. It is these central cells which are first built when each comb is begun. As in stelocytarus nests, the regular arrangement is normally lost after $1\frac{1}{2}$ -2 life-cycles have elapsed.

4. ESTIMATING THE AGE OF A NEST.

The fundamental unit in estimates is the developmental period from egg to adult. When the first cocoon in a comb is just ready to produce a young

wasp, the age is just one developmental period ($= 1$). If any cells are being used for a second time the age must be more than 1, and it is usually possible, by the appearance of the cells and the contents of the combs, to estimate whether the age is greater or less than 2. No attempt was made to guess the age of nests older than 3, e.g. in such species as *Polybia rejecta* (Fab.), with long-lived colonies. Possibly something could be done by counting successive layers of silk left by old cocoons.

There are, unfortunately, no data for the lengths of the egg, larval and cocoon stages in any Polybiine. There are little reliable data for any VESPIDAE, the best probably being Janet's (1895 : 125-7) for *Vespa crabro* L., in France. In this species the figures are much affected by the large variations in external temperature and by the seasonal growth of the nest. In August, with nearly optimum conditions, the egg, larval and pupal periods were 5, 12 and 13 days. Schwarz (1931 : 26), studying *Polybia occidentalis spilonota* Cam. (recorded as var. *scutellaris*) in Panama, suggests that the development seems not to differ much from that of *Vespa*. In default of more reliable data, it has been assumed that the egg, larval and cocoon stages occupy, respectively, one-fifth, two-fifths and two-fifths of the developmental period.

The age of a comb containing only eggs is, then, 0-0.2, mean 0.1; of one with eggs and larvae, 0.2-0.6; and of one with eggs, larvae and pupae, 0.6-1.0. If the respective numbers of eggs, larvae and pupae are a , b and c , it has been taken that the age of the comb is $0.6 + \frac{c}{a+b+c}$ (0.4). If $c = 0$ (no pupae present), the age of the comb is $0.2 + \frac{b}{a+b}$ (0.4). If no larvae are present, the age is taken as 0.1.

When a comb is being used for a second time the fraction of the age above 1.0 must be calculated only from those cells which are being used a second time, i.e. normally those in a circular central area. When the stages are distributed at random, as often happens by age 2+, the whole of the comb contents were used to estimate the probable excess over 2.0. Where several combs are present, the age of the nest is estimated from the upper, older combs. In some species, however, the initial colony consists of more than one comb, and in these the colony was treated as a whole.

The estimates arrived at are evidently only approximate, especially as the numbers of eggs and larvae were only estimated; but they seem to have a real use in analysing the data.

If the total length of the developmental period was known, the figures obtained could be converted into days, but for many purposes this is not necessary.

It might have been expected that the stages, when the censuses of a number of nests were averaged out, would tend to be found in proportion to their duration. However, when this averaging was done for 56 nests of 12 species, the proportions of egg : larva : cocoon came out at about 0.4 : 0.3 : 0.3. Since all direct observations suggest that the egg-stage is shorter than the pupal stage, it must be assumed that this method is invalidated by larval mortality and, perhaps to some extent, by variations in oviposition-rate or in nest-temperature (cf. also p. 105).

5. NEST-CYCLES.

While, as in the last section, the developmental period is a convenient measure of the age of the nest, the more fundamental unit for the species is the time taken to produce the first males and young queens. It would appear that in this respect there are two main types of behaviour in the POLYBIINAE. In such wasps as *Polybia occidentalis* (Oliv.) (most subspecies), *P. bistriata* (Fab.), *Metapolybia*, *Protopolybia minutissima* (Spin.), and *Mischocyttarus*, as in *Polistes*, after a few developmental cycles (nests of age 2.0-3.0), males and queens are produced, and the colony breaks up. The species of *Vespa* s.l. living in temperate climates essentially follow this plan. There is no evidence that the end of their colonies is due to the weather, much more that it is due to the death of the queen. Colonies of *V. sylvestris* Scop. and *V. rufa* L. end long before the autumn frosts which, in the other species, only hasten the disintegration which has already started. The ending of the small *Polybia* colonies after a relatively short period is even more curious. Weather can play no part in it and the presence of a number of egg-laying queens makes it less likely that the disintegration is due to their senility (cf. discussion, p 127.).

The other type of colony, confined to the tropics, is seen in such species as *Polybia rejecta* (Fab.), *Protopolybia pumila* (Sauss.), *Epipona tatra* (Cuv.), and probably *Synoecca surinama* (L.), and at the limits of the tropics in *Polybia occidentalis* var. *scutellaris* (White) and *Brachygastra lecheguana* (Latr.). These wasps make nests which last a long time, probably some years. In *P. occidentalis* var. *scutellaris* nests possibly last as long as 25 years (Lucas, 1867 and 1885), and one was observed intermittently for 4 years by Bruch (1936). In *E. tatra*, FitzGerald observed a nest which lasted 2 years without altering in size and, according to Lacordaire, this species probably sends out swarms at yearly intervals. Cyclical reproduction of this kind is presumably typical of all the species in this group.

6. NATURE OF THE CARTON.

It is characteristic of the social wasps to make their nests of vegetable materials, worked up into a sort of paper. The ZETHINAE (solitary) are a connecting link, mostly (perhaps all) using vegetable materials; while some *Odynerus* s.l. use resin, nearly all the EUMENINAE build with mud. All the EUMENINAE which make elaborate mud constructions have very long narrow mandibles; the social POLYBIINAE, POLISTINAE and VESPINAE, and the ZETHINAE have short, broad mandibles. There is considerable variation in the quality of the carton made by the VESPIDAE. It is most paper-like in the VESPINAE (cf. Weyrauch, 1936 : 402) and in the POLISTINAE. It is coarser in the POLYBIINAE, the particles are less chewed up, and in *Mischocyttarus* they are often large, and joined with a great deal of salivary secretion, sometimes leaving transparent "windows," or even holes in the walls. Similar windows are a feature of the envelope of *Metapolybia cingulata* (Fab.) (Rau, 1933 : 52). *Apoica* is peculiar in making a nest of felted plant-hairs. Moebius (1856) illustrates the constituents of the carton in a number of species.

7. THE USE OF NESTS IN CLASSIFICATION.

While all the genera of POLYBIINAE (except perhaps *Stelopolybia* Ducke, p. 69) can be defined by satisfactory morphological characters, the search

for these has been encouraged by the differences in nest-architecture which were often discovered first. As Duce (1905a : 1) has pointed out, it is unlikely that Saussure (1852) would have founded the genus *Synoea* if he had not known that the nest was very different from that of *Polybia*, for he did include in that genus many other species whose nests, then unknown, have since been shown to be equally distinct. Duce (1910 ; 1914) has been the great protagonist of the view that nest-architecture is the clue to the recognition of the phylogeny of social wasps. In these works will be found the phylogenetic diagram which eventually appeared in its most complete form in Wheeler's well-known work (1923 : 71).

It is perhaps worth while quoting Duce's views on this point (1910 : 450), "La nidification des guêpes sociales a évolué de formes simples jusqu'aux formes compliquées de phragmocyttares parfaits et des stelocyttares calyptodomes (voir les tableaux synoptiques des genres) ; cette évolution accompagne d'une manière très évidente l'évolution morphologique des insectes qui les construisent, ce qui rend relativement facile l'établissement de genres vraiment naturels. L'évolution morphologique a été, dans la famille des Vespides, convergente, les formes à intellect le plus hautement développé ayant les caractères morphologiques les moins différenciés ; chez les Vespides sociales polygames cette opposition entre l'évolution du corps, convergente, et celle de l'intelligence, divergente, nous apparaît clairement."

The principle criticism which might have been made of Duce's views was that the morphology of the wasps, in spite of the great advances which he himself made, had been very inadequately studied. As far as morphology was concerned, in general only very superficial features could be used to support his views on phylogeny. A preliminary study of the structure of wasps has shown that a very large number of additional characters can be used which may well put our views on their phylogeny¹⁰ on a much sounder basis. Unfortunately, the completion of this morphological study will take some years, and it was thought better not to hold up the present paper any longer. It is, however, worth pointing out now the reasons why it is unlikely that nests are quite as good a guide to phylogeny as Duce thought.

The genus *Stelopolybia* evidently caused Duce himself some difficulty. Three species make stelocyttares calyptodomous nests, whereas the others make stelocyttares gymnodomous nests. Several attempts have been made to find generic characters to distinguish these groups (Richards, 1943) but it does not appear that any really satisfactory ones exist.

The most fundamental breach, however, in Duce's theory was made by Carl (1934). He found (see also Van der Vecht, 1940) that certain species of *Ropalidia* make nests of an elaborate type resembling the phragmocyttares nests of S. American POLYBIINAE. Hitherto, it had been supposed that all species made very simple stelocyttares gymnodomous nests. These species which make such elaborate nests cannot, at most, be more than generically separated (at present they are in the same genus) from the species which make nests of the simplest type.

Finally, we noticed in *Mischocyttarus* (Richards, 1945 : 302), that while

¹⁰ In particular, it seems now most unlikely that the various groups of social wasps (except possibly the STENOGASTRINAE) can have been separately derived from the solitary species.

there is a general correlation between the morphological classification and the nest-structure, there are a number of exceptions. In a few cases, species which are extremely closely allied make very different types of nests and a number of distinct species make similar nests.

It is clear that here, as elsewhere, the characters derived from a study of behaviour are neither more nor less reliable guides to phylogeny than those derived from a study of adult morphology. In each case an exhaustive examination must be made and those features picked out which, in combination, give the most consistent classification. In detail we are on surer ground with morphology, for it has been studied for a longer period by more workers. We have as yet no general principles for deciding which elements in behaviour are likely to be of phylogenetic importance, though it often seems that small details are more reliable than superficially larger differences.

In studies of this type, where no fossil evidence is available, we are dealing with probabilities, and the value of our speculations depends mainly on the number of facts which support them. It cannot be too much emphasised that most insect groups are insufficiently studied, that the number of characters, which may be quite adequate for accurate identification, may be too few for reliable phylogenetic speculation. But when, as a result of really thorough study, a classification based on a wide variety of characters is built up, then genera with many morphological characters in common must be regarded as phylogenetically closely allied; otherwise no subject of theoretical taxonomy is possible at all.

8. METHODS OF TAKING NESTS.

A proper understanding of Vespid biology, particularly of nest-dynamics, entails examining the complete contents of a number of nests in all stages of development. The vast majority of the adult inhabitants must be captured, and at least a sample dissected. As we gained some experience in the way to capture whole colonies, we give some suggestions.

Only a few of the POLYBIINAE are really aggressive, though most of them will occasionally give a bad sting, especially if members of a large nest. Of the species we dealt with, it is only really essential to wear a hat, veil, gloves and coat when taking nests of *Stelopolybia* (tree-nesting species), *Protopolybia pumila* (Sauss.), and possibly *Polybia rejecta* (Fab.). *Synoecca surinama* (L.) has a bad reputation, but Rau (1933: 124) describes a very successful capture. We came to the conclusion that on the whole 6.0 a.m. is the best time of the day to take nests. The wasps are often somewhat less active then and are probably nearly all inside or on the envelope of the nest (but cf. *Stelopolybia fulvo-fasciata* (Deg.)). However, apart from *Stelopolybia*, very few wasps are seen leaving or entering the nest during the middle of the day; in fact, we were always puzzled as to how all the material for running a large colony was brought in. In 1929 (Oxford University Expedition) a number of nests were taken at night, but in general the difficulties of working in the dark far outweigh any supposed advantages. Very few, if any, of the wasps seem to sleep at night, and they seem adept at flying up the beam of a flashlamp.

If, in capturing a nest, a number of wasps is lost, they often form a swarm either on the old nest-site (especially if even a small part of the envelope has been left) or near it (usually on the same branch, but sometimes on an adjacent

one). A visit to the spot within 24 hours of taking the nest will often enable one to capture all the wasps that were lost on the first attempt. In several cases the swarm flew away to some quite different locality after sitting in the original place for about a day.

From the point of view of capture, the nests we studied can be classified into five types.

(1) *Metapolybia cingulata* (Fab.). The nests of this species are flat and are attached directly to the tree-trunks or walls. The wasps are not at all aggressive and the colonies are small (< 100 wasps). Probably the most effective method is to catch the wasps about 3 at a time in glass tubes. If this is done carefully most of them remain seated on the envelope and can be persuaded to fly into the tube. Eventually, the envelope must be opened up and the wasps which remain inside captured also. If the nest be revisited about half an hour later, any odd ones which escaped will be caught then. It is worth recording the order in which wasps were captured, since queens seem to stay in the nest until last. Attempts to anaesthetise nests by pressing a tin containing chloroform against a circular ring of cotton-wool were rarely successful.

(2) Nests attached to large leaves with no part of the envelope embracing a twig (*Stelopolybia pallens* (Lep.), *Mischocyttarus*, *Polybia* spp., *Protopolybia* spp.). Nests of this type, unless unusually large, are best taken in a large glass-bottomed pill-box. The wasps always fly to the glass bottom, whereas, if an ordinary tin is used, they fly to the light and many escape as the lid is removed through the leaf, especially as they can squeeze through the smallest crevice. Most of the POLYBIINAE have little hesitation in leaving the nest in a body, especially from the smaller nests.

(3) Nests attached to twigs, or very large nests on leaves (*Polybia occidentalis* (Oliv.), etc., *Brachygastra*, *Protopolybia pumila* (Sauss.), *Stelopolybia pallens* (Lep.)). Even if not too large, nests of this type cannot be taken successfully in pill-boxes, since the twig prevents the top from being forced on until many wasps have escaped. An extremely successful method of taking such nests is as follows. Trim away surrounding branches, so that the nest hangs free and a butterfly-net can be held beneath it; give the wasps a little time to settle down again. Then cut the supporting twig through, suddenly, with a pair of pruning scissors. The nest falls into the net and the wasps scarcely fly out until it hits the bottom of the net. The net must then be gripped quickly and tied up tightly with string. It is more difficult than would be supposed to prevent the wasps from squeezing their way out; it is essential that there should be no small tears in the net. The nest and wasps can be anaesthetised in the net in a large tin. Often every single wasp can be successfully captured in this way. This method can only be applied where it is possible to cut the twig through in one snap of the scissors, and where the net can be held beneath it. But it is sometimes almost as successful to cut the twig and very quickly carry the nest out of a bush and drop into a net outside. If the end of the supporting twig projects far beyond the nest, the twig must always be pruned near the nest.

(4) Hanging nests on thick branches (*Polybia rejecta* (Fab.)). The nests were attached 15 ft. from the ground on trees infested with Dolichoderine ants. The wasps were too aggressive for the nest to be approached very closely on

a ladder. The method we adopted was to tie a net onto a long pole, and a cutlass onto another. If one person then holds up the net, another can knock the nest into it. The net must then be brought to ground as rapidly as possible and tied up. About half to two-thirds of the inhabitants may be captured in this way. As the nests are very populous (1500 upwards) this may be a large enough sample, but it is always uncertain whether it is a random one. The difficulty in this method is to cut off the nest near enough to its point of attachment to the bough and to prevent the escape of wasps between the time the nest falls into the net and the moment when it is possible to tie it up.

The wasps which are lost usually form a temporary swarm on or near the nest-site, and a number of them may be captured here later.

(5) Nests in hollow trees (*Stelopolybia fulvo-fasciata* (Deg.)). We only saw two nests of this type and only had the opportunity to take one. The wood was hard in both cases and the entrance relatively small (area at most 56 cm.). We did not evolve any very good way of dealing with these nests. The wasps are very aggressive and they differ from most other POLYBIINAE in that many workers are continually passing in and out. The colony appears to become active very early in the morning (before 7.0 am.). Possibly a visit in the dark, when, presumably, most of the workers would be at home, would have been advantageous. The entrance might then have been stopped up with cotton-wool and the nest anaesthetised. Or perhaps the introduction of cyanide, which would kill the workers inside and also those returning, would be equally effective. Blocking the entrance in the day-time makes an area of several metres round the nest unapproachable without a veil, etc. for about 3 days. After the wasps have been caught or killed, the opening up of the hollow tree may be very laborious.

9. DEFINITION OF CASTES.¹¹

The worker caste in social Hymenoptera consists of unfertilised females, normally incapable of fertilisation and normally with undeveloped ovaries. In ants and in the honey-bee the worker is separated from the queen by discontinuous morphological characters. Where, however, such clear-cut distinctions are absent difficulties arise. It may be impossible to distinguish workers from young queens while in some POLYBIINAE the ovaries show all stages in development. It becomes necessary, therefore, to have some way of drawing a line, as little arbitrary as may be, between queens and workers. It is conducive to clarity in argument to lay down hard and fast definitions and to apply them strictly, particularly when giving censuses of nest-inhabitants. In the present study all individuals in whose receptaculum sperm were found were called *queens*. Fortunately, in most species, the queens so defined have ovaries very much more developed than those of their nest-mates. For in a number of nests the wasps had to be preserved in alcohol and dissected later (e.g. all nests from Kaieteur); under these conditions it is no longer possible to make out the sperm in the receptaculum. Here queens were defined solely on the development of their ovaries; on analogy with the other nests this is usually

¹¹ This subject is discussed in more detail later (p. 105). The information given here shows how our material was classified in 1937.

pretty reliable, e.g. *Polybia bistriata* (Fab.), nest 145 (p. 56), 1 ♀ (ovary with 19 eggs), 12 intermediates (2-3 large eggs), 38 workers (with filamentous ovaries).

In such species as *Stelopolybia pallens* (Lep.) or *Protopolybia minutissima* (Spin.) there is a more or less complete transition in ovarian development from worker to queen. In such nests only the examination of the receptaculum shows which are queens; if sperm are absent, individuals with ovaries like those of the queens are termed intermediates. In spite of statements by H. von Ihering (e.g. 1896:159), we found no case in which there was any differentiation in the size of the receptaculum as there is in *Apis*.

We have used the term *intermediate* for any individuals in which sperm were absent but the ovaries were more developed than in the workers. In some cases the intermediates may be young queens but this is probably very rarely so unless males are also found in the nest. All our observations support the view that males and queens are produced at about the same time, after a period in which only workers (and intermediates) have been reared.

In some species, particularly in large colonies (e.g. *Polybia rejecta* Fab., *Protopolybia pumila* (Sauss)), queens which have been laying for some time can easily be picked out by eye, since the abdomen becomes swollen and paler in colour. In the other species this change is imperceptible.

It is of importance to discover whether all females are at first alike and only become queens and workers as a result of fertilisation, egg-laying and differential feeding of the adult, or whether there is differential feeding of the larvae so that the two castes emerge from the pupa essentially different though later diverging further. We have endeavoured to answer this question by biometrical studies of series of queens and workers defined by dissection. The characters measured are not thought necessarily to have any biological significance, but are ones which are convenient to measure. If, for instance, as in *Polybia occidentalis* (Oliv.), the worker has more wing-hooks (hamuli) than the queen, this at least shows that the castes must have emerged from the pupa differing to this extent. The character is a measure of pre-imaginal differentiation. The statistical tests of significance are those given by Fisher (1948).

10. EXPLANATION OF TABULATED NEST-DATA.

For each species of which we were able to study several nests, we have prepared a table of the nest-contents and calculated certain ratios which will be needed in the final discussion. The first column gives the serial number of the nest. The second the number of cells; if there was more than one comb, the cells in the top comb are given first and the numbers for the other combs below it. Next, the total number of wasps which were captured, followed by an estimate, made at the time, of the number seen to escape. This estimate is very rough, but is better than nothing; the number escaping has never been added to the total caught when calculating cell/wasp ratios, etc. The fifth column gives the number of queens, which is an estimate if only a sample of the wasps was dissected (i.e. in most nests with more than 150 wasps). The range and the mean number of ovarian eggs in the queens comes next. Then the number of intermediates, and, in some cases, a record of the eggs in their ovaries. Then the number of workers and of males. The next three columns

give the number of cocoons and estimates of the number of larvae and eggs, separate figures being given for the different combs where necessary. In most of the nests only the cocoons were counted, but notes were made of the areas of empty cells and of those with eggs and larvae. It was realised afterwards that it would have been worth the expenditure of the time required to make accurate counts but, in a two-months' stay, this could only have been done at the expense of something else. It must be understood, therefore, that the figures for larvae, eggs and empty cells are very approximate. The estimates, however, were made at the very start of writing up the results and are unlikely to be biased by any theory which was formed later. The next column gives the age of the nest, calculated by the methods explained in section 4. Then followed 4 ratios which help in the discussion of nest-dynamics, *viz.* cells/wasps (= total of all female castes); larvae/workers + intermediates; eggs/queens; eggs/total of ovarian eggs in all queens.¹² In all the tables the nests are arranged in order of age.

11. THE NATURAL HISTORY OF THE GENERA AND SPECIES, PRINCIPALLY THOSE FOUND IN BRITISH GUIANA.

Keys for the identification of the British Guiana social VESPIDAE (except *Mischocyttarus* Sauss.) are given by Bequaert (1944); *Mischocyttarus* was dealt with by Richards (1945). It is only necessary, therefore, to give a few supplementary taxonomic notes. Besides listing our own Guiana records, we have included records from the British Museum collection, particularly where they extend the recorded range in British Guiana. A brief note is included on the few South American genera which have not yet been found in British Guiana. We have also attempted to revise the records of P. Cameron (1912) and Bodkin (1917) so far as their material was available for study. The group of species allied to *Polybia occidentalis* (Oliv.) presents special difficulties, and its taxonomy is dealt with in Appendix 1, and the species of *Apoica* Lep. are revised in Appendix 2.

1. *Pseudochartergus* Ducke, 1905.

This genus includes 3 South American species, one of which is found in British Guiana. The species have been revised by Bequaert (1938: 194).

The nest is stelocytarous and gymnodomous, and consists of a single comb hidden between leaves (*e.g.* of banana) and attached to them by several pillars (Ducke, 1910: 465).

1. *P. chartergoides* (Gribodo, 1891) var. *cinctellus* (Fox, 1898).

This form was described from British Guiana by Cameron (1912) as *Charterginus pallidiballeatus* (type ♀ in coll. B.M.), and recorded by Bodkin (1917) as *C. "pallidilineatus"*. Bequaert (1944: 264) records it from Kartabo and we captured 6 ♀, Mazaruni Settlement, Colony House, on windows, 18.viii.-25.ix.1937. Illustrations of the nest have been published by Ducke (1905b: pl. 1, fig. 2) and by R. von Ihering (1904: pl. 6, fig. 11).

¹² As far as is known all the VESPIDAE have three pairs of ovarioles, except the VESPINAE, which have six.

2. *Charterginus* Ducke, 1904.

This genus, which has recently been revised by Bequaert (1938: 99), includes 4 S. and C. American species, of which one has been found in British Guiana.

The nest is a peculiar variety of the stelocytтарous calyptodomous type, in which there is a single comb, supported beneath a leaf by a single, broad petiole. The entrance is on the dorsal side of the nest (between it and the leaf), and the passage perforates the comb. In *C. fulvus* Fox the envelope is drawn out into long points, like a star, but in the two other species of which the nest is known the envelope is simple, of a brilliant whitish colour.

1. *C. huberi* Ducke, 1904.

This species was described from British Guiana by Cameron (1912) as *Polybia fulvicauda* (type ♀, in coll. B.M.). Bequaert (1944: 264) records it from "Sources of Essequibo R. and Warratuk." We captured one specimen, Mazaruni Station, second growth forest, 12.viii.1937, ♀.

The nest is illustrated by Ducke (1905b: pl. 2, fig. 8). It is mushroom-shaped with whitish carton.

3. *Protopolybia* Ducke, 1905.

There are at least 9 species in C. and S. America, and they have been revised by Bequaert (1944a); 5 of them are found in British Guiana, 2 or 3 rather commonly.

The nest is a peculiar modification of the stelocytтарous calyptodomous type. In smaller nests (e.g. *P. holoxantha* (Ducke) and *P. minutissima* (Spin.)) there are 1 or 2 combs. The first is attached beneath a leaf by several pillars and surrounded by an envelope with a lateral exit-hole. The second comb, when present, is built on the envelope of the first, and has a separate exit-hole. The larger nests (e.g. *P. pumila* (Sauss.)) become very irregular. The envelope may include a number of leaves and twigs, and the attachment of the first comb to a branch may be sessile, perhaps secondarily. The arrangement of the combs may become irregular so that their number is difficult to count, but, as far as can be made out, each comb has a separate exit-hole. The lower combs are suspended from the upper ones by a number of pillars. Reid (1942: 312) describes the larvae of two of the species, but the one recorded as *P. sedula* was really *P. pumila* (Sauss.) (mis-identification by O.W.R.).

1. *P. holoxantha* (Ducke, 1904).

Cameron (1912) first recorded this species from British Guiana (2 ♀ in coll., B.M.), and Bequaert (1944: 266) gives the following localities: Kamakusa; Moraballi Creek, Essequibo R.; Penal Settlement. His second record was from specimens captured by the Oxford University Expedition: nest 1715, 4.ix.1929, beneath leaf of *Eschweilera sagotiana* Miers, 60 ft. up (found when felled). In 1937, we found 3 nests: No. 142, Potaro R., Amatuk, 31.viii., beneath leaf of Aroid, 7 ft. up; no. 143, same data beneath leaf of palm, 8 ft. up; no. 83, Bartica-Potaro Rd., 14 miles from Bartica, 20.viii., beneath leaf of climbing Aroid, 10 ft. up, found when felled (T. A. W. Davis).

For various reasons, none of the 4 nests was very fully investigated. In

all of them the carton was tough and fibrous, and in nos. 83 (pl. 1, fig. 1) and 1715 with brown and white streaks arranged concentrically. The cells were 2.0 mm. in diameter and 5.0-6.0 mm. deep. The cocoons were flat-topped and not domed above the cells. Nest 142 was a young nest, of one comb, without an envelope, but it was lost before it was described: 42 wasps were captured, probably half the total. They consisted of 22 ♂ and 20 queens or intermediates (not examined for sperm). The ovarioles of these had no more than 2-3 small eggs and were not clearly separated from those of the workers. Nest 143 was a much older nest of 190 cells in a single, elongate comb. There were 64 cocoons, a number of larvae, mostly large, and very few eggs: 38 wasps were captured, but probably as many were lost. There were 5 males and 33 workers or intermediates (not examined for sperm). Few had really filamentous ovarioles and there was a continuous gradation up to those with 2-3 small eggs in their ovarioles. Nest 83 (pl. 1, fig. 1) had 253 cells, nearly all containing cocoons, the others empty. There were only 23 wasps left in the nest, and these were workers.

Nest 1715 hung beneath the mid-rib of a leaf, high up a tree. After felling, the nest and 4 wasps were obtained, and 2 more emerged a week later. The comb was only 2.5×1.2 cm., and consisted of 60 cells with 10 cocoons.

Ducke (1905b: pl. 3, fig. 11) illustrates a nest from Brazilian Guiana: Oyapoc, of irregular shape but with a striped envelope like the two which we found. Bequaert (1944a: 104) also briefly describes a nest. *P. holoxantha* seems to be typically a species of relatively unmodified high rain-forest. The male has not yet been described; it differs from the female as follows:

Microscopic silvery pubescence of clypeus denser, clypeus a little narrower, antennae with 13 unmodified segments, flagellum rather more darkened dorsally, ventral half of eyes considerably broader and more swollen, tempora narrower, more retreating, POL: OOL = 2:3 (not 1:3); shallow punctures of mesonotum considerably more evident, dark markings tending to be more distinct; abdomen with 7 visible segments.

2. *P. minutissima* (Spinola, 1851).

Two varieties of this species are recorded from British Guiana by Bequaert (1944: 266), but the vars. *minutissima* (Spin.) and *binominata* (Schulz) seem to be connected by various intermediates. As, however, all our specimens but one had at least traces of spots on the propodeum, they are probably best placed under the second name. Bequaert records it from Kartabo, Georgetown and "Demerara." Cameron (1912) recorded it as "*Polybia pygmaea* F." Although we found 5 nests, we only caught 4 specimens away from their nest—Potaro R., Kaieteur Savannah, 5.ix. and 7.ix., 2 ♀; Mazaruni Station, clearing, on windows of Colony House, 17.viii., 1 ♀; and on rotten bread-fruit on ground, 26.viii., 1 ♀ (the only specimen unambiguously belonging to to the var. *minutissima* (Spin.)). The nests were found as follows: Nest 168, Potaro R., Kaieteur Savannah, 3.ix., beneath leaf *Brochinia micrantha* (Baker) Mer., 2 ft. up; nest 211, Potaro R., Takeit-Kaieteur Trail, 6.ix., beneath large leaf, 4 ft. up; nest 57, Mazaruni Station, 20.viii., beneath leaf of *Clusia*, on a large tree in clearing, 5 ft. up; nest 124, Mazaruni Station, clearing, 28.viii.; beneath leaf of mango, 10 ft. up; nest 84, Mazaruni Station, clearing, 23.viii., on *Citrus*, 12 ft. up. This species (in this variety at any

rate) is confined to open country and only just penetrates into light second-growth forest; it was not found in 1929 in the dark forest at Moraballi Creek. The 5 nests are treated in order of estimated age. Three (84, 168, 211) had the envelope of a light chocolate-brown colour with white streaks, and 2 (57, 124) of a light stone-grey. The texture was fibrous. The cells were 2.0×5.0 mm., and the cocoons were flat-topped, not projecting beyond the cells.

Nest 168 was seen on 2.ix., when the envelope had hardly been begun and was represented by a narrow rim. The nest must, therefore, have been recently started. The envelope was nearly completed by 3.ix. (pl. 1, fig. 2). It then consisted of a single comb of 540 cells, nearly all containing eggs, and a few containing drops of a honey-like liquid. All the wasps in the nest (226) were captured, but on the next day 14 more, presumably foragers, were found seated on the old nest-site. After preservation in alcohol, 100 wasps were dissected; 78 were queens or intermediates, 22 workers. It was not possible to distinguish queens and intermediates; in some the ovarioles were rather more developed than in others, but none looked like a typical *Polybia* queen. There were usually 1-3 somewhat larger eggs, but they were relatively small. The specimens were not well preserved and even the workers may have contained some disintegrated eggs.

Nest 57 (pl. 1, fig. 3) consisted of 2 combs; an upper one of 590 cells and a lower one of 960. The upper comb had a central area of cocoons, surrounded by larvae and by a few eggs, with a large outer ring of empty cells. The lower one was only partly covered by the envelope; the covered part contained 53 cocoons, many larvae and eggs, and the uncovered part, 2 cocoons, many eggs and many empty cells in the part furthest from the envelope. It would appear that the upper comb and the covered part of the lower one were constructed at about the same time, while the uncovered part was made later. Ninety-nine wasps were captured and dissected, and about 30 escaped. There were 49 workers, 24 intermediates (no sperm), and 26 queens (with sperm). Eight of the workers had Gregarines in the body-cavity. The number (total) of enlarged eggs in the ovarioles of the queens was as follows (no. of queens in brackets): 3 (5), 4 (9), 5 (9), 6 (3). The intermediates had 1-2 developing eggs clearly larger than the other rudiments, but they did not look ripe and were smaller than those of the queens.

In nest 124 there were 2 combs, a larger upper one of 458 cells and a small lower one of about 100 cells, mostly containing eggs. The upper comb had a central group of 183 cocoons, surrounded by larvae and eggs. Fifty-one wasps were captured, and on dissection were found to include 3 queens (sperm present; 6, 6, 7 eggs), 25 intermediates (no sperm), and 23 workers. The ovaries of the intermediates tended to intergrade with those of queens, but few of them had eggs which looked ripe. The queens each had some eggs larger than any seen in the intermediates.

Nest 211 (pl. 1, fig. 4) was bun-shaped, 8.7 cm. in diameter, with an entrance to each comb on one side, towards the tip of the leaf from which it was suspended. There were 2 combs, each of 2204 cells, those in the upper one having been used before. Eggs, larvae and pupae were scattered throughout, and some cells contained drops of honey. The lower comb also contained all stages throughout, except that there were no cocoons in the outermost rings. All the wasps, 693, were captured and 100 were dissected. These consisted

of 55 workers (3 containing Strepsiptera), 32 intermediates (2-4 well-developed eggs), 3 queens (12, 13, 16 eggs) and 10 males. Later, all the wasps were examined externally, but no more Strepsiptera were discovered. This was a considerably older nest than the three previous ones and the ovarian development of the queens seemed to have diverged considerably further from that of the intermediates.

Nest 84 consisted of one comb of 278 cells, with 16 cocoons, but otherwise empty. Nearly all the wasps were lost but the 6 captured consisted of 2 queens (sperm present; 9, 10 eggs), 4 workers, and 3 males. This would appear to have been in a late stage of development, probably already sending off swarms, and with the development of the brood almost finished.

The details of these nests are shown in Table 2.

TABLE 2.

Nest data for *Protopolybia minutissima* (Spin.).

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	Eggs	♂	♂
168	540	226	14	176	1-3			50	0
57	590 960	99	30	26*	3-6, 4-4	24	1-2	49	0
	1550								
124	458 [100]	51	12	3*	6, 6, 7	25	1-4, 2-3	23	0
	558								
211	2204 2204	693	0	21	12-16, 13-7	222	2-4	381	69
	4408								
84	278	6	Most	2*	9, 10	0		1	3

Nest no.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ Wasps	Larvae/ ♀ + Interm.	Eggs/ ♀	Eggs/ ovarial eggs
168	0	0	500	40	1.0	2.4	0	2.3	1.4
57	82 55	250 295	100 500	178 110	.66	10.6	6.8	23.0	5.3
	117	545	600	288					
124	183 0	100 0	175 80	0 20	0.76	10.9	2.1	78.0	12.4
	183	100	255	20					
211	281 253	923 951	1000 1000	0 0	1.65†	6.4	3.1	95.0	7.0
	534	1874	2000	0					
84	16	0	0	262	1-3				

* Presence of sperm verified.

† Estimated from the two combs together; possibly the real age was 2.65.

No obvious external difference was observed between queens, intermediates and workers. Wing-lengths and hamuli numbers were measured in 26 queens, 26 intermediates and 37 workers. The averages are shown below. None of the

differences are significant. Five other characters were also measured in 12 ♀, 12 intermediates and 12 ♂ (from 5 nests), using a screw-eyepiece micrometer. The following characters did not differ significantly: the minimum width of the vertex, the length of the mesonotum, the length of the 1st abdominal tergite, *a*, from the dorsal muscle to the point where the sides diverge, and, *b*, from this point to the posterior margin. The mean widths of the posterior margin of the 1st abdominal tergite were: queens 0.737, intermediates 0.718, workers 0.702 mm. The queens and workers differed significantly (*P* between 0.02 and 0.01).

Earlier accounts of the nest will be found in Ducke (1905*a*: pl. 3, fig. 10), Bequaert (1944*a*: 107), and Rau (1933: 87, figs. 41 and 42) (as *P. sedula*).

Mean wing-lengths and hamuli numbers in 26 specimens of the castes of *P. minutissima*.

Caste	Wing-length (mm.)	Hamuli no.
Queen . . .	4.69	5.54
Intermediate . . .	4.62	5.50
Worker . . .	4.61	5.38

Var. *sedula* (Saussure).

Bequaert (1944) does not record this variety from British Guiana though it is known from all adjacent territory. *Polybia nana* Cameron, 1912 *nec* Saussure, 1867 (syn. n.) belongs to a profusely yellow-marked form of this variety. The yellow is of an orange tint and extends to nearly the whole face, the pronotum, behind and below the transverse keel, and nearly the whole mesopleuron. Besides 2 ♀ (*P. Cameron* coll.), both marked "*Polybia nana* type," there is one female "British Guiana" (*Rodway*). Bequaert (1944*a*: 109) gives references to descriptions of the nest. Probably all the large nests ascribed to this variety by Ducke (1910) really belong to *P. pumila* (Sauss.) (*q.v.*), but his figure (1905*a*: pl. 3, fig. 9) probably refers to the true *sedula*.

3. *P. amarella* Bequaert, 1944.

This species was described by Bequaert (1944: 267; 1944*a*: 113) from British Guiana: source of Essequibo R., and from Colombia. In the British Museum collection there is one specimen—BRITISH GUIANA: New River, boundary mark 82, 1300 ft., 12.v.1938, ♀ (*C. A. Hudson*).

4. *P. emortualis* (de Saussure, 1855).

The typical form (type, ♀, in coll. B.M.) was described from Brazil; there is a second specimen—Obidos, 22.xii.1904, ♀ (*A. Ducke*). All the British Guiana specimens belong to the var. *duckei* (R. du Buysson, 1905); which Bequaert (1944: 270) records from British Guiana: Upper Essequibo R., while noting that Ducke reported it from Brazil: Bahia and Peru: Iquitos. The following specimens are in the collection of the British Museum:

BRITISH GUIANA: 4 ♀ marked as types of *Charterginus rufo-ornatus* Cameron, 1912 (syn. n.); 2 ♀ (*G. E. Bodkin*); Essequibo R., Moraballi Creek, 13.viii.1929, ♀ (Oxford Univ. Exped.). Bodkin (1917) recorded the species as "*Protopolybia laboriosa* Sauss."

One nest, no. 349, was found, Mazaruni Station, second growth forest,

27.ix. It was on a small tree about 9 ft. above the ground. Many leaves of the tree were inhabited by the ant, *Dolichoderus (Hypoclinea) bidens* (L.) (det. H. St. J. K. Donisthorpe). These ants make carton nests, either in the form of bags beneath the leaves or by joining overlapping leaves with carton. This diffuse nest covered much of the tree, especially the parts 30–40 ft. up, and the nearest cartons to the wasps' nests were 10–12 ft. away. If the tree was shaken the vicious ants swarmed all over the leaves and made it very unpleasant for any intruder. On the other hand, the wasps when moderately disturbed, unlike all other social species studied, retired into their nest and left defence to the ants. This behaviour has been previously recorded for this species by Ducke (1907 : 166, pl. 2, fig. 2 ; 1910 : 470, fig. 1), who also states that the wasps make a double envelope, the outer one imitating the ant-carton. The envelope of nest 349, however, was single. It was interesting that the Sphecid wasp, *Trigonopsis affinis* Sm. var. (nest previously undescribed), had built two groups of mud cells on the underside of leaves right amongst the ants. This nest, made of pale mud, was almost indistinguishable from the ant-cartons when seen from the ground.

The envelope and cells of *P. emortualis* were made of rough, thick, greyish-brown, crumbly carton, not fibrous, but made of small bits of vegetable matter stuck together. The cells were 3.0 mm. in diameter and 5.0 mm. deep. In the other three species of this genus examined the carton of the envelope was very thin, smooth, papery and capable of bending without breaking.

The nest was flattened, $5.0 \times 2.5 \times 1.2$ cm., attached to the leaf by one big central pillar and two smaller ones. The leaf was hanging so that the long axis was nearly vertical and the exit-hole of the nest was on one side of the long axis, and 2.0 mm. in diameter. There were 134 cells, mostly with eggs, but a few with small drops of a honey-like liquid. Fifty wasps were captured and dissected, but a considerable number, perhaps as many again, escaped. There were 20 ♀ and 30 probable intermediates. In none of them was sperm found in the receptaculum, but the intermediates showed some degree of ovarian development ; the frequencies of different numbers of egg-rudiments being as follows (number of wasps in brackets) : 1 (2), 2 (3), 3 (10), 4 (10), 5 (5). Presumably the queen, or queens, escaped.

5. *P. pumila* (de Saussure, 1863)

Bequaert (1944a : 122) records the typical form of this species from BRITISH GUIANA : Kartabo ; Bartica ; Sources of Essequibo R. ; also from Colombia, Venezuela, Dutch Guiana, Brazil, Peru and Bolivia. In the British Museum collection there are also specimens from ARGENTINA : Alto Parana, Bemberg, 15–17.iii.1934, ♀ (*K. J. Hayward*), and PARAGUAY : Puerto Bertoni, ♀ (*A. de W. Bertoni*) (det. as *P. sedula*). New British Guiana records are : New River, Boundary mark 82, 1300 ft., 12.v.1938, ♀ (*C. A. Hudson*) ; Mazaruni Station, clearing, on windows of Colony House, 11.viii.–26.ix.1937, 22 ♀ ; nest 302, on twig of mango tree, 25 ft. up, 23.ix.1937 ; Potaro R., Warratuk, nest 158, 31.viii.1937, 2 ♀ preserved.

All the specimens we obtained were from clearings or from very open forest. Most of the previous records of the biology of this species have been recorded under the name "*P. sedula*," and are inextricably confused with those of

P. minutissima (Spin.). Bequaert (1944a: 125) publishes some interesting observations made by Weyrauch in Peru. The nest described by R. von Ihering (1904: 247), from Peru, sounds like the ones that we saw in Guiana. Nest 302 (pl. 1, figs. 5 and 6) was subspherical, $15.0 \times 12.5 \times 12.5$ cm., and the envelope was light-stone colour, with light-brown streaks, of fibrous texture. The dorsal surface of the combs was darker with chocolate-brown streaks. Many leaves were incorporated in the nest. There were approximately 5 very irregular combs, really arranged in a spiral. There were many exits between the combs but it was impossible to be sure that there were no connections between them. The cells were 3.0 mm. wide and 5.0 mm. deep, and the cocoons projected 1.0 mm. below the rims of the cells. When the combs were broken up, the number of cells was estimated at 21,600, by measuring the area of the fragments and counting the number of cells in some of them. The general appearance of the nest was that of some *P. minutissima* nests (nos. 57 and 124), but larger.

Seven thousand and eighty seven wasps were taken, and about 150 lost. Forty wasps were dissected at the time, and consisted of one queen (13 eggs, sperm present), 27 intermediates (ovaries with 0-4 moderate-sized eggs, no sperm), 10 workers (ovaries more or less filamentous), and 2 males. Later, another 60 wasps were dissected from alcohol, and consisted of one queen (17 eggs), 41 intermediates, 17 workers, and one male, *i.e.* in 100 wasps, 2 queens, 68 intermediates, 27 workers, 3 males. It was then found that queens could be picked out by eye owing to their more swollen abdomen: three picked out at that time had 13, 14 and 18 eggs (sperm present); later, 88 were picked out, making 93 in the whole nest, with an average ovarian egg number of 15.

The combs contained numerous eggs, larvae and cocoons arranged at random. Some "honey" was present in the cells of the lowest comb. The nest was evidently in an advanced state of development and ready, or almost ready, to give off swarms. A tentative analysis of its contents is given in Table 3.

The wing-lengths and numbers of hamuli were compared in 20 queens,

TABLE 3.

Analysis of the contents of nest 302, *Protopolybia pumila* (Sauss.).

No. of wasps	7087.0
Males, 3 per cent.	213.0
Queens, direct count	93.0
Average no. of ovarian eggs per queen, 15; total	1395.0
Intermediates, 68 per cent.	4853.0
Workers, 27 per cent.	1928.0
Cells (estimated)	21,600.0
Cocoons "	7200.0
Larvae "	7200.0
Eggs "	7200.0
Cells/Wasps	3.1
Larvae/workers + intermediates	1.1
Eggs/queens	77.4
Eggs/ovarian eggs	5.2
Estimated age	2+

20 intermediates and 20 workers. The queens are clearly differentiated from the other two types of female, which are sensibly similar (Table 4).

TABLE 4.

Wing-lengths and hamuli-numbers in females of *Protopolybia pumila* (Sauss.).

	Wing-length (mm.)			Hamuli					Mean
	4.5	5.0	5.5	5.	6.	7.	8.	9.	
Queens	0	1	19	0	6	12	1	1	6.85
Intermediates	0	20	0	7	8	5	0	0	5.90
Workers	1	19	0	3	15	2	0	0	5.95

A second nest, no. 158, was found at Warratuk, on the branch of a small tree, 10 ft. from the ground. It was about 28.0 × 18.0 × 15.0 cm., made of whitish carton, with an exit-hole between the layers of the envelope on one side, near the bottom. The wasps were very aggressive and bad stingers. The nest was not further studied.

4. *Protonectarina* Ducke, 1910.

The single species of this genus, *P. sylveirae* (Saussure, 1853), is not likely to be found in British Guiana as it is an inhabitant of eastern, especially south-eastern, S. America. According to Ducke (1910:477), it is found from BRAZIL: Ceará to N.W. Argentina, but the British Museum collection includes 3 ♀ labelled, possibly wrongly, "Upper Amazon."

The nest is subspherical, phragmocyttarous, very like that of *Brachygastra* (*g.v.*), and considerable quantities of honey are often stored. R. von Ihering (1903a:152; 1904:250) and Bertoni (1911:122) have published observations on its biology, but the nest has not, apparently, been illustrated.

5. *Brachygastra* Perty, 1833.

(= *Nectarina* Swainson and Shuckard, 1840.)

There are 7 American species, one of which just penetrates into the southern United States. Four of them are found in British Guiana.

The nest is always phragmocyttarous but there is a good deal of variation in the shape. Reid (1942:314) describes the larva of *B. scutellaris* (Fab.).

1. *Brachygastra angusti* (Saussure, 1854).

Bequaert (1944:272) records the typical form from BRITISH GUIANA: sources of the Essequibo R., and it is widespread in S. America. In the British Museum collection are the following specimens: BRITISH GUIANA: New River, 750 ft., 20.ii.1938, 13 ♀ (C. A. Hudson).

The nest has been described by R. von Ihering (1904:232), Ducke (1910:482), and Bertoni (1911:115), but does not seem to have been illustrated. It is ovoid in shape, rather like that of *Polybia occidentalis* (Oliv.), but with a rougher, brittle envelope. The combs are rather convex, with the exit-holes excentric. R. von Ihering describes a nest of 7 combs, which was 10.0 cm. high and 13.0 cm. maximum diameter.

2. *Brachygastra lecheguana* (Latreille, 1824) var. *velutina* Spinola, 1841.

The variety differs from the typical form in the greater development of golden pubescence. It occurs mixed with the typical form, but seems to be commoner in the rain-forest. All the Guiana specimens belong more or less clearly to the variety which was first recorded from British Guiana by Erichson (1848 : 590) [as *B. aurulenta*]. Bequaert (1944 : 272) records it from British Guiana : Arakaka, and the species as a whole from Arizona and Texas to Northern Argentina. In the British Museum are specimens from BRITISH GUIANA : Essequibo R., Ondernaming, ii.1916, ♀ (*G. E. Bodkin* and *L. D. Cleare*, Jr.) ; North-west district, Issororo, vii.1916, ♀ (*C. B. Williams*). The second specimen is probably one recorded by Bodkin (1917).

The nest of the species has often been described (summary in Bequaert, 1933 : pls. 27 and 28), and is of a spherical, phragmocytarous type. The wasp is also well-known for the large amount of honey it stores, at any rate in the drier parts of its range. In Mexico, it is kept in a semi-domesticated state (du Buysson, 1905). Du Buysson showed, by dissection of alcoholic specimens, that about 17 per cent. of the nest-inhabitants are queens. The colonies soon become large, with thousands of wasps, and if not destroyed for their honey, persist for several years. In Mexico, new, small nests are found in the spring, after the rains, but swarming may not be seasonal in the rain-forest. Du Buysson's observations suggest that the general organisation of the colony resembles that of *B. scutellaris*, described below, though the Mexican nests probably become much larger.

3. *Brachygastra scutellaris* (Fabricius [1805]).

Bequaert (1944 : 272) records the typical form and the var. *myersi* Bequaert, 1943, from British Guiana, the first from Mazaruni Station and Kartabo, the second from Mt. Roraima. As shown below, there is some evidence that the colour-pattern of var. *myersi* may be related to caste-differentiation when both it and the typical form occur in one nest. There is a third form, var. *rufiventris* (Saussure, 1854), of which the type, ♀, from Pará is in the British Museum collection. This seems to be a variety in which the reddish coloration of the callows of the ordinary forms persists into the mature adult. The following specimens are in the British Museum collection : var. *scutellaris* (Fab.), BRITISH GUIANA : North-west district, Issororo, vi.1915, ♀ (*G. E. Bodkin*) ; Mazaruni Station, clearing, on windows of Colony House, 17.viii.1937 ; Potaro R., Kaieteur Savannah, nest 180, on twig of shrub, 2 ft. up, 3.ix.1937 (most wasps) ; nest 186, on twig of Melastomaceous shrub, 3 ft. up, 4.ix.1937 (most wasps). Var. *myersi* Beq., BRAZIL : Ega, ♀. BRITISH GUIANA : Kartabo, ix.1922, ♀ (*M. D. Haviland*) ; nests 180 and 186 (some wasps).

The specimen from Issororo was recorded by Bodkin (1917), but Cameron's (1912) specimen from the Potaro has not been traced. The species appears to be associated with clearings or open, scrubby woodland. The nest has been described and figured by Moebius (1856 : 23, pl. 15, as *Chartergus*), Ducke (1907 : 156, pl. 3, fig. 6), and Rau (1933 : 137, fig. 65).

The two nests which we found were very similar, pyriform in shape, broadening downwards, about 10.0 cm. long and 7.5 cm. at the broadest. The entrance was at one side, between the bottom comb and the one above it. The envelope

and combs were brown, made of non-fibrous, crumbly carton, composed of small pieces of vegetable material, stuck together. The cells were 2.6 mm. wide and 4.0 mm. long, *i.e.* relatively very shallow. The cocoon caps were attached to the rim of the cell and were only slightly domed in the centre, the wasps themselves being short and broad.

Nest 180 (pl. 1, figs. 7 and 8) was taken in the rain at 7.0 a.m. (sun time), and no wasps were lost. It contained 863 wasps, of which 100 were dissected from alcohol. They consisted of 8 queens (sperm not seen) with 12, 13, 13, 14, 17, 17, 18, 21, mean 15.6, developed eggs in their ovaries, 30 intermediates (see below) and 62 workers. Twenty-five newly emerged (*i.e.* more or less uncoloured) specimens all had worker ovaries. In the whole nest, therefore, there were probably 69 queens, 259 intermediates and 535 workers.

The nest consisted of 5 combs with the following features:

1. (= top). 138 cells. 31 cocoons; cocoons, larvae and eggs scattered throughout.

2. 286 cells. 123 cocoons; cocoons in centre, eggs and larvae outside.

3. 468 cells. 122 cocoons; eggs, larvae and cocoons scattered throughout.

4. 690 cells. 500 cocoons; central area with many eggs; some of the pupae just ready to emerge. A few cells with a little honey.

5. (= bottom). 743 cells. All with eggs.

Totals: 2325 cells, 776 cocoons, approx. 1200 eggs, 349 larvae.

All the cells had been used before, except those in comb 5, and possibly the cells with cocoons in comb 4.

Nest 186 contained 876 wasps and none, or very few, were lost: 200 were dissected later from alcohol. They included 13 queens (6.5 per cent.) with 8, 9, 10, 10, 11, 11, 11, 12, 12, 12, 13, 14, 16, mean 11.5, developed eggs in their ovaries, 87 intermediates (43.5 per cent.), 100 workers (50 per cent.). In the whole nest there were, therefore, about 57 queens, 381 intermediates, and 438 workers.

The nest consisted of 6 combs with the following features:

1. 160 cells. A few cocoons, mostly eggs.

2. 218 cells. Larvae and cocoons mixed.

3. 400 cells. Central area of cocoons and young larvae, outer area of young larvae and eggs.

4. 520 cells. Cocoons, large larvae and eggs, mixed together.

5. 530 +, say, 600 cells. Centre mostly with eggs and a few cocoons; outer area mostly cocoons, with an extreme outer row of larvae.

6. 684 cells. All eggs.

Totals: 2582 cells and approx. 661 cocoons, 1289 eggs, 632 larvae. All the cells had been used before except in comb 6.

The following ratios can now be established:

Nest	Cells/wasps	Larvae/workers + intermediates	Eggs/queens	Eggs/ovarial eggs
180	2.69	0.44	17.4	1.1
186	3.06	0.77	22.2	2.0

The ovaries of the workers were typically filamentous, with no formed eggs visible under low magnification ($\times 15$). A few, however, had some slightly developed eggs. The intermediates had the ovaries more or less

developed, and no very sharp line separated them from the workers on the one hand, and the queens on the other. The ovaries were bigger than those of the workers and nearly always had some distinctly formed eggs. The queens had ovaries much larger and the eggs were larger and riper. The number of developed (= countable) eggs was enumerated in 40 of the intermediates, with the following result :

Frequency	No. of eggs								Total	Mean
	0.	1.	2.	3.	4.	5.	6.	7.		
	2	0	5	6	5	13	8	1	168	4.2

In the remaining 47 intermediates it was noted that the ovaries had 1-6 larger rudiments, whereas in the workers the ovarioles were filamentous or with very small rudiments. The queens and intermediates were almost discontinuous: queens 8-16, mean 11.5 eggs; intermediates 0-7, mean 4.2 eggs.

These two nests seem to be in very much the same state of development. They seem to belong to the type of *Polybia rejecta* (Fab.) rather than of *P. occidentalis* (Oliv.), i.e. a number of developmental cycles are completed before any males are produced. It is probable that the colonies are potentially long-lived, just as those of *B. lecheguana* (Latr.) are in Mexico and Argentina.

The workers, intermediates and queens all had fore-wings of length between 5.5 and 6.5 mm. The figures for the numbers of hamuli on the hind-wings were as follows :

		Hamuli no.	6.	7.	8.	9.	10.	Mean
N. 180	Queens .		0	0	3	3	2	8.89
	Intermediates		1	7	15	7	0	7.93
	Workers .		0	10	13	7	0	7.90
N. 186	Queens .		0	2	8	3	0	8.08
	Intermediates		0	6	23	0	1	7.87
	Workers .		2	9	16	2	1	7.70

The difference between the mean numbers in queens and workers is significant in nest 180, and in the two nests together (in both cases $P < 0.01$) but not in nest 186 alone. It may also be significant that the individuals which were picked out as intermediate between queens and workers in ovarian development are also intermediate in hamuli number.

A study was also made of the colour-pattern in relation to the castes. In nest 186, browning or reddening of the proximal part of the abdomen seems to be independent of the distribution of yellow pigment, and was never quite so far developed as in the var. *rufiventris* (Sauss.), in which, presumably, the red colour is retained throughout life. In the present nest reddened specimens formed 12.2 per cent. of the whole. In the 200 which were dissected they only occurred amongst those which had filamentous ovarioles, of which they made up 36 per cent. This higher percentage probably partly arises from the effect of dissection on abdominal colour. It seems likely that the relatively small degree of reddening found in the wasps from this nest was due entirely to immaturity, and it was, therefore, never found in individuals with developed

ovaries, for all emerge with them filamentous (on analogy with other Hymenoptera and from the 40 dissected which emerged after the nest had been taken).

Four stages in the reduction of the yellow pigment of the scutellum were recorded: (a) scutellum entirely yellow, (b) dorsal surface of scutellum $\pm$ half yellow, (c) dorsal surface of scutellum with a posterior central yellow spot, vertical surface from all yellow to nearly all black, (d) scutellum all black. The form *d* very nearly corresponds to the var. *myersi* Beq., but in the extreme form of the variety, not found in this nest, the yellow band of the scutellum may be absent, and the yellow bands on the abdomen are paler and more or less reduced. The frequencies of these forms are shown in Table 5.

TABLE 5.

Proportion of colour forms *a-d*, in nest 186 of *B. scutellaris* (Fab.).

Form	200 dissected (absolute numbers)		Whole nest (%)	Expected (%)
	♀ + interm.	♀		
<i>a</i> . . .	25	35	34	30.0
<i>b</i> . . .	21	33	23	27.0
<i>c</i> . . .	23	22	24	22.5
<i>d</i> . . .	31	10	18	20.5

From the sample dissected there is clear evidence that those individuals whose ovaries are capable of development tend to have less yellow on the scutellum. It should be noted that the pigment is fully developed on emergence from the pupa and does not appear to vary during the adult stage. The percentage of the forms actually observed in the whole nest differed somewhat from what would be expected from the proportions of the colours in the sample dissected (see Table 5, column "Expected"). This is probably due only to sampling errors.

In nest 180, 100 specimens were dissected, and 10 of these had the anterior part of the abdomen more or less reddened. In the undissected specimens 7.7 per cent. showed this character. A much higher proportion of wasps in this nest had the scutellum entirely yellow, but as far as the figures go they suggest that the specimens with better developed ovaries have *more* yellow pigment on the scutellum (Table 6). It is possible that there is no consistent relation between colour and ovarian development in *B. scutellaris*, but only a study of further nests can decide.

TABLE 6.

Proportion of colour forms *a-d*, in nest 180 of *B. scutellaris* (Fab.).

Form	100 dissected			Whole nest (%)
	Queens	Interm.	♀	
<i>a</i> . . .	8	25	39	74
<i>b</i> . . .	0	4	13	14
<i>c</i> . . .	0	0	7	11
<i>d</i> . . .	0	1	3	1

4. *Brachygastra bilineolata* Spinola, 1841.

Bequaert (1944 : 273) has recorded the typical variety from "Demerara" and Georgetown, and the var. *antillarum* (Provancher, 1883) from the Rupununi R.; the var. *surinamensis* Bequaert (1943b : 306), described from Dutch Guiana, is represented in the British Museum collection by 2 ♀—BRITISH GUIANA : Ituni Savannah, ii. 1919 (*A. A. Abrahams*). In this form very nearly the whole body is pale yellow. The British Museum also has specimens of the typical variety : BRITISH GUIANA : R. Puruni, v. 1916, 2 ♀ (*G. E. Bodkin*); no precise locality, 3 ♀ (*J. Rodway*; *P. Cameron* coll.).

Bodkin (1917 : 309) recorded a nest of the typical form (as var. *moebiana* Sauss.) from Georgetown Botanic Gardens. It was attached to a sugar-cane "arrow," and was $\frac{3}{4}$ in. deep and $1\frac{1}{2}$ in. greatest diameter. The nest has also been described and figured by Ducke (1904 : pl. 1, fig. 1, var. *smithii* (Sauss.)); 1905 : pl. 1, fig. 1, var. *smithii* (Sauss.)). It is spherical with an exit-hole in the form of a lateral slit, corresponding to emarginations at the edges of the combs. Ducke never saw one with more than 4 combs.

6. *Chartergus* Lepeletier, 1836.

There are two closely allied S. American species, one of which has been found in British Guiana.

The nest (Saussure, 1854 : pl. 33, figs. 1 and 2; R. von Ihering, 1904 : 239, fig. p. 234) is the best example of the elongate, cylindrical, phragmocytтарous type, made up of a number of combs, each one with a central exit-hole leading to the entrance in the centre of the bottom of the envelope. The carton is whitish, and very hard and tough.

1. *Chartergus chartarius* (Olivier, 1791).

Bequaert (1944 : 274) records this species from "Demerara" and from Georgetown. Bodkin (1917 : 309) has the following observations : "A fairly common species in the interior. The nest of this species is a well-known object, and has been previously described by a number of authors. They are prized by many colonists as 'curios,' and fetch a very fair price in Georgetown. These nests may sometimes be seen attached to the branches of trees overhanging the river. The taking of nests is by no means an easy matter, as the insects resent any interference with their home. Nests, however, which overhang the river may be taken by getting a native to ascend quietly the particular tree to which the nest is attached, and with one well-directed blow of a sharp cutlass sever the branch bearing the nest so that it falls into the river, whence it is eventually retrieved as soon as the wasps have left. An unsuccessful blow, however, spells disaster, and there is a case on record where such an incident occurred, and the unfortunate native, rather than suffer, jumped into the river many feet below, and thus evaded the infuriated wasps."

The nests were seen overhanging the Essequibo R. in 1929, but it was not possible to get at them. They are often associated with the large carton nests of the ants, *Ateca* spp. (DOLICHODERINAE) (cf. p. 98).

7. *Clypearia* de Saussure, 1854.

There are two S. American species neither of which has yet been recorded from British Guiana. The nest belongs to the type which has been called

(p. 6) astelocytтарous. A comb is built directly on a branch of a tree, and an envelope which, in this genus is little domed is constructed on the branch from near the edge of the comb. The exit-hole is at one end. Extra combs may be added at this end, with the envelopes forming a series of annexes to the original one (Ducke, 1904 : pl. 1, fig. 4 ; 1910 : fig. 6).

8. *Synoeca* de Saussure, 1852.

Bequaert (1944 : 274) now recognises 3 species in this genus, and all of them have been recorded from British Guiana.

The nests, so far as they are known, are astelocytтарous and essentially like that of *Clypeaia*, but with the envelope more domed. The wasps have a bad reputation for stinging (cf. Rau, 1933 : 127) and they are resembled in colour by a number of other insects.

1. *Synoeca surinama* (Linnaeus, 1767).

There are two forms of this species.

(a) Var. *surinama* (L.).

Colour often blackish rather than blue. Clypeus and, nearly always, mandibles dark. Scutellum without outstanding bristles. Propodeum much less punctated. Mesopleural suture tending to be stronger below the punctiform fovea.

Apparently the characteristic form of the Guianas (including Trinidad and, according to a British Museum specimen which needs confirmation, B.W.I. : Grenada, 1.iii.1914, ♀ (*Dr. Balfour*)) and of Amazonia.

(b) Var. *cyanea* (Fabricius, 1775).

Colour always blue. Clypeus and mandibles partly ferruginous. Scutellum with very short outstanding bristles. Propodeum much more punctated, sometimes not very different from that of *S. virginea* (Fab.). Mesopleural suture more obsolete below the punctiform fovea. Posterior margin of scutellum often narrowly testaceous.

Found in areas surrounding the home of the var. *surinama* (L.) and perhaps overlapping it in S. Brazil, viz. (in coll. B.M.) Mexico, Guatemala, Nicaragua, Panama, S.W. Ecuador, Colombia, Venezuela, Brazil (Ilha Santo Amaro ; Rio Grande do Sul), Paraguay.

The specimens from Rio Grande do Sul (4 ♀) and from Paraguay (1 ♀) are structurally intermediate between the two forms (*e.g.* in propodeal sculpture and scutellar bristles), but the clypeus is entirely ferruginous. Apart from these females, only 8 out of 29 have the clypeus entirely ferruginous. The published records of these varieties need critical revision.

In British Guiana only the var. *surinama* (L.) occurs, and Bequaert (1944) records it from Arakaka, Mazaruni Station (= Penal Settlement), Bartica, Rockstone, Kartabo, Georgetown, Kamakusa, Berbice Savannahs, and Blairmont. The British Museum collection includes a number of unlocalised Guiana specimens. According to Bodkin (1917 : 309), it is commoner on the coastlands than in the interior, and this is also our experience. It is not found in tall forest, and a characteristic site is Georgetown Botanic Gardens, where a fine nest was seen in 1929. The nest consists of several combs enclosed in a number of large, domed envelopes, placed end to end ; it may

be as much as a metre long, with 5 compartments (Bertoni, 1911: 117). The envelope is very characteristically transversely ribbed. The nest has been figured by Moebius (1856: pl. 1), R. von Ihering (1904: 242, fig. 2), du Buysson (1906: pl. 16), Ducke (1910: fig. 7). Rau (1933: 121, figs. 55-7) gives an interesting account of the var. *cyanea* (Fab.) in Panama. He found it associated with nests of the ant, *Azteca trigona* Forel; such associations with ants are further referred to on p. 99. He also describes the barbed sting, with which a painful wound can be given. Bodkin notes that the wasps feed on fallen fruit and on certain flowers, and Bertoni (1911: 117) gives a list of the flowers and fruits visited in Paraguay. The species of this genus seem to be more anthophilous than most other Polybiines, at least they are more often seen on flowers. The foundation of new colonies has been described by FitzGerald (1938: 189).

Perhaps because of its conspicuous colour-pattern and powerful sting *S. surinama* (L.) is mimicked by a number of other insects in South America. Ducke (1910: 460), Bertoni (1911: 117) and FitzGerald (1939: 105) have noted the following: VESPIDAE, *Eumenes* sp., *Montezumia rufidentata* Sauss., *M. azurescens* Spin., *Zethus coeruleipennis* (Fab.), *Polistes goeldii* Ducke; SYRPHIDAE, *Cerioides facialis* Kertész.

2. *Synoeca virginea* (Fabricius [1805]).

Besides the characters given by Bequaert (1944: 275), this species can be separated from the form of *S. surinama* var. *cyanea* with the most strongly punctured propodeum, by the shape of the outer valve of the propodeal orifice. In side view it is much more pointed in *S. virginea*. The interantennal impression is also much more often produced upwards, towards the median ocellus.

Bequaert records the species in British Guiana, from Kartabo, Mazaruni Station, Bartica district, and source of the Essequibo R., and Bodkin (1917) states that it is uncommon in the interior. Richards (1947) recorded a female, Mazaruni Station, second-growth forest, 23.ix.1937, as prey of the Asilid fly, *Erax titan* Bromley. We obtained the following additional specimens in 1937: Mazaruni Station, second-growth forest, 23.ix., 27.ix., 2 ♀; clearing, 21.vii., ♀; on *Lantana Camara* L., 23.viii., ♀; on *Waltheria indica* L., 17.viii. and 19.viii., 2 ♀; Potaro R., Kaieteur Savannah, 1-10.x., 10 ♀; forest on edge of Savannah, 4-10.ix., 3 ♀.

The species is not found on the coastal plain, and it would seem to be characteristic of openings in areas of rain-forest in the Amazons-Guiana region. The nest, according to Ducke (1910: 488), is like that of *S. surinama* but with the envelope more brittle and not ribbed. The only one illustrated, however, (Ducke, 1907: pl. 1, fig. 1), is an abnormal one. It has been found near those of ants or of other wasps (see p. 99). The wasps are resembled in colour by the paler forms of *Polybia affinis* du Buyss.

3. *Synoeca chalybea* de Saussure, 1852.

Bequaert (1944: 276) records this species from BRITISH GUIANA: Shudihar R. It is also found in the Amazonian region, and in the British Museum collection are 7 females of a slight variant from PANAMA: Bugaba, 800-1500 ft. (*Champion*).

9. *Metapolybia* Ducke, 1905.

There are two American species but only one has been found in British Guiana.

The nest is astelocytтарous, and the envelope is very little domed, the cells being shallow. Apparently the envelope may arise either from the edge of the comb or from the substratum a little way from it. On vertical tree trunks the entrance is at the top. According to Ducke (1910: 488), additional irregular combs may be built, but this was never observed in Guiana. In the characteristic position, on tree trunks, the envelope usually harmonises very perfectly with the bark, but on sheds, etc., the nest is very conspicuous. As first noted by Rau (1933: 52), the envelope usually has a large number of small, transparent spots, made, perhaps, of dried saliva or at any rate of something very different from the carton. Reid (1942: 317) has described the larva of *M. cingulata* (Fab.).

1. *Metapolybia cingulata* (Fabricius [1805]).

Bequaert (1944: 277) records the species from Kartabo and Bartica. According to Bodkin (1917: 308), it is not found on the coastal plain and commonly makes its flattened nests on the beams of houses where it is not conspicuous. The British Museum collection has specimens from BRITISH GUIANA: Issororo, Rockstone, Moraballi Creek, and New River. In 1937 we obtained the following: Mazaruni Station, second-growth forest, 14.ix., 1 ♀; clearing, 24.ix., on white-washed cowshed wall, 12 ft. up, nest 311; clearing 12.viii., on south side of *Eucalyptus* tree, 6 ft. up, nest 11; clearing, 28.viii., on trunk of mango (*Polybia rejecta* tree, p. 40), 10 ft. up, nest 122; clearing, 28.viii., on trunk of mango, 20 ft. up, nest 123; clearing 27.viii., on trunk of mango, 15 ft. up, nest 115; clearing, 20.viii., beneath side branch of large tree, 15 ft. up, nest 58.

Outside Guiana the species is known from Trinidad, and from Mexico to Peru, Bolivia and Paraguay. Moebius (1856: pl. 11) gives a coloured figure of the nest, and FitzGerald (1938: 188, pl. 3, fig. 10) describes how it is built. The largest one he saw in Trinidad was 92.0×13.0 cm.; our nest 11, which was only 14.0×6.0 cm., contained 493 cells, so FitzGerald's nest may have contained as many as 7000 cells.

Of the 6 nests which we found in 1937, 5 were in the usual site on tree trunks where they were very inconspicuous, and one on the white-washed outer wall of a cowshed, where it was conspicuous, though resembling a lump of mud. The nests all consisted of a single comb attached directly to the substratum by the bottom of the cells, whose long axes were horizontal, or nearly. The envelope, which was only a small distance away from the distal ends of the cells, was normally made of material which harmonised perfectly with the surrounding bark. Both the envelope and the cell-walls had a number of "windows"—small gaps in the carton filled with a transparent material, possibly dried salivary secretion. The comb and the envelope tend to narrow at the upper end where the small entrance is found. The envelope arises from near the outer walls of the peripheral cells, except at the entrance. The carton is not fibrous, but made of small vegetable fragments stuck side by side, very

thin but somewhat pliable. The cells were 9.0×2.75 mm., except in nest 11, where they were 3.0 mm. in diameter. The cocoon-caps were flat and sunk 1.0–2.0 mm. below the distal ends of the cells. The nests enumerated below are arranged in order of estimated age.

Nest 311 (pl. 2, figs. 9 and 10) was on a shed beneath a slightly projecting window ledge. There was a central area of 207 deep cells and a peripheral area of very shallow ones. The central area contained cocoons with some larvae amongst them. The peripheral ones contained eggs. A few cells had drops of honey distally to the larvae. The envelope was produced into a sprout-like projection, not enclosing cells.

Nest 11 (pl. 2, figs. 11 and 12) had a pear-shaped envelope (narrow at the top) 14.0×6.0 cm. The entrance was 1.0 cm. in diameter. The envelope was raised 1.5 cm. above the bark and enclosed 493 cells. The centre of the comb contained cocoons with 16–20 eggs amongst them. Nearer the entrance the cells mainly contained large larvae, and between these and the cocoons were many small larvae. The lower part of the comb appeared to be a recent extension; it consisted of shallow, incomplete cells, mainly empty. The wasps were caught one by one, in tubes, as they left the nest. The first 37 were workers; no. 38 was a queen with 4 eggs and about 20 rudiments in each of her 6 ovarioles; nos. 39–55 were workers; nos. 56 and 57 were apparently intermediates, each containing 3 eggs. The spermathecae were not examined.

It was noted in the week 11–17.viii. that this was the only occupied nest seen, though 5 deserted ones were found. This was probably because the envelope soon disintegrates and the exposed cells are then conspicuous. In Barro Colorado Island, Panama, Rau (1933: 47) found only young nests in late August and early September; it was not until late September that he found nests with large larvae.

Nest 122. The central part of the comb contained many cocoons and the periphery some eggs. This was the only nest in which males were found.

Nest 123 was a small one, most of whose wasps had apparently already left. All the cells were being used again and were mostly empty with a few scattered cocoons and eggs.

Nest 115 was 7.5×6.3 cm. in area and contained 312 cells, nearly all of which were being used again. There was a central area of 29 cocoons and round them a large number of eggs. There were only 6 wasps present, so presumably a swarm had already left. Two of the wasps were queens and could be distinguished by their slightly larger size and browner abdomens. On dissection, they contained 10 and 11 eggs in their ovaries, though only in the first could sperm be found in the spermatheca. The other had a distended spermatheca but no sperm; possibly they were exhausted.

Nest 58 again showed many cells being used again. About one-quarter of the cells contained cocoons but there were no eggs, and no queen was found. Perhaps this nest had also given off a swarm; or else it may have lost the queen through some accident and the colony had disintegrated.

The wing-lengths and hamuli-numbers were examined in 23 queens and 23 workers from 5 nests. The mean figures were: wings, 6.35 mm., ♀ and ♂; hamuli, 7.43 ♀, 7.30 ♂. This difference is clearly not significant and no other external indication of caste was noted.

The data of the 6 nests are collected in Table 6A.

TABLE 6A.

Data from six nests of *Metapolybia cingulata* (Fab.).

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	Eggs	♀	♂
311	[250]	54	4	12*	10-18, 14-3	0		42	0
11	493	57	6	1	24	2	3	54	0
122	[120]	106	12	5*	9-17, 12-0	0		73	28
123	27	2	2	1*	9	0		1	0
115	312	6	1	2	10, 11	0		4	0
58	156	37	0	0		0		37	0

Nest no.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♀ + interm.	Eggs/ ♀	Eggs/ ovarial eggs
311	53	47	100	50	0-71	4-6	1-1	8-3	0-6
11	82	261	50	100	1-10	8-6	4-7	50-0	2-1
122	56	0	30	34	1-2	1-1	0	6-0	0-5
123	9	0	9	9	1-2	13-5	0	9-0	1-0
115	25	0	10	187	>2	52-0	0	50-0	4-8
58	40	0	0	116	>2	4-2	0		

* Presence of sperm verified.

10. *Synoecoides* Ducke, 1905.

There are two American species, recently revised by Araujo (1944). Neither has yet been found in British Guiana, though *S. depressa* Ducke occurs in Amazonia.

The nest (Ducke, 1907: pl. 3, fig. 7; Araujo, fig. 5) is a spherical one, of the phragmocyttrous type, with a lateral exit-hole. The wasps are rare, and very little is known about them.

11. *Epipona* Latreille, 1802.

There are two species, one confined to Central America, the other occurring from Costa Rica to Amazonia.

The nest has been described by Cuvier (1797: 57, fig. 1A), de Saussure (1854: pl. 32), R. von Ihering (1904: 244) and Ducke (1907: pl. 2, fig. 5). It is phragmocyttrous, becoming broader downwards, with the exit-hole very much on one side.

1. *Epipona tatra* (Cuvier, 1797).

We collected two specimens in 1937: Mazaruni Station, clearing, in Colony House, 24.ix., 1 ♀; on flowers of *Lantana Camara* L., 17.viii., 1 ♀. These are the first records from British Guiana.

According to FitzGerald (1938: 189, pl. 2, fig. 7), the nests, in Trinidad, are found high up in trees and persist for a long time. One was inhabited for 2 years without increasing in size. Lacordaire (1838: 508) gives an early account, much of which is so interesting as to be in great need of verification and amplification. He saw many colonies in Cayenne, only in woods, chiefly

second-growth near plantations. They were usually placed amongst leaves 2 or 3 ft. from the ground. The colonies did not dissolve each year. In the rainy season, from January to mid-June, only entirely completed nests were found; they were dangerous to interfere with, so only a few were examined. In January the cells contained only larvae, but the numbers of this stage were much reduced in March and April, and they were almost absent by the end of May. About mid-June, with the return of good weather, nests in the course of construction began to be found, about a dozen females often being seen at work. Larvae were found almost as soon as the cells were finished, and the nests grew gradually by the addition of combs. In September they have mostly finished, and towards the end of November it was rare to find one which was incomplete. The old nests of the previous year co-existed with them, with the full complement of inhabitants. New larvae began to be abundant again in September or October. The suggestion of annual swarming in a region so near the Equator is very interesting, but it is difficult to be sure that Lacordaire identified the wasps correctly in all cases.

According to Westwood (1837), *E. tatua* (as *Chartergus nidulans*) is parasitised by *Phasgonophora* (as *Chalcis*) *pyramidea* (Fab.).

12. *Polybia* Lepeletier, 1836.

There are about 40 species of this genus which is found from Mexico to Buenos Aires, and forms an important part of the Neotropical fauna. Twenty-three species are here recorded from British Guiana.

All make phragmocyttarous nests of various types, in the group of *P. emaciata* Lucas, of mud instead of carton. Reid (1942:308) describes the larvae of 4 species.

1. *Polybia gorytoides* Fox, 1898.

Bequaert (1944:281) records this species from BRITISH GUIANA: West bank of Demerara R.; Bartica. There is one female from British Guiana in coll. British Museum, without precise locality.

According to Ducke (1905b:679), the nest, which has not been figured, resembles that of *P. micans* Ducke (p. 38).

2. *Polybia liliacea* (Fabricius [1805]).

This species is widespread in British Guiana but not very common. Bequaert (1944:282) records a number of localities and also gives some notes on the nest. It is sausage-shaped, truncate at the lower end, and very large, up to a metre long. It has been referred to by de Saussure (1858:ex.) and by Lucas (1867). It is found from Colombia to Ecuador, Peru, Bolivia and Amazonia. The following specimens are in the collection of the British Museum: BRITISH GUIANA: Essequibo R., Moraballi Creek, dark forest, 6.xi.1929, 1 ♀ (*Oxford Univ. Exped.*); Mazaruni Station, clearing, 15.ix.1937, 1 ♀; high forest, prey of the Asilid, *Mallophora* sp. ♂ (det. H. Oldroyd), 16.viii.1937 (*Richards and Smart*); Cuyuni R., Kamaria landing, 23.xi.1929, 2 ♀ (*Oxford Univ. Exped.*); North-west district, Issororo, vi.-vii.1917, 6 ♀ (*C. B. Williams*); New River, 25.ii.—15.iii.1938, 3♀ (*C. A. Hudson*); Upper Courentyne R., ix.1935, 1 ♀ (*G. A. Hudson*); no precise locality, 2 ♀ (*J.*

Rodney; *P. Cameron* coll.). Also in coll. Dept. Agric., Ituré Savannah, ii.1919, 1 ♀ (*A. A. Abrahams*); Essequibo R., Rockstone, 31.xii.1913, 1 ♀ (*G. E. Bodkin*).

It appears to be mainly a forest species. Its striking pattern of black and pale yellow is repeated in the next species and in the following other VESPIDAE: *Polistes liliacius* Sauss., *P. pacificus* Fab. var., *Mischocyttarus pseudo-mimeticus* (Schulz), *Montezumia liliacea* Grib., *M. liliaciosa* Grib. (Ducke, 1910: 460; FitzGerald, 1939: 105).

3. *Polybia striata* (Fabricius, 1787).

(= *P. sycophanta* Gribodo, 1891).

Bequaert (1944: 282) records this species from Kartabo and Warina in British Guiana. It is also known from Colombia to Bolivia and Brazil. The following specimens are in the collection of the British Museum: BRITISH GUIANA: North-west district, Issororo, vi.1915 and 15.vi.1916, 2 ♀ (*C. B. Williams*); Berbice R., Plantation Providence, 13.ix.1919, 1 ♀ (*G. E. Bodkin*).

Bequaert gives some notes on the nest, which is white and spherical and placed high up in a tree. FitzGerald (1938: 186, pl. 2, fig. 6) found a nest in Trinidad in its earliest stages. It had 4 combs, the top one of 75 cells, the bottom one of 500, and a few eggs in the top one only.

4. *Polybia jurinei* Saussure, 1854.

Recorded by Bequaert (1944: 283) from BRITISH GUIANA: Kartabo, and known from Colombia to Bolivia and Brazil. The British Museum has the following specimens: BRITISH GUIANA: Upper Courentyne R., King Frederick William IV Falls, 14-23.iii.1936, 1 ♀; Kartabo, vi.1922, 1 ♀ (*M. D. Haviland*); North-west district, Issororo, vi.1915, 1 ♀ (*G. E. Bodkin*).

The nest has been described by Ducke (1904: 350; 1905b: 678). It is campanulate or rounded, with a smooth solid envelope. It is found in the forest.

5. *Polybia sulcata* Saussure, 1854.

This species has not previously been recorded from British Guiana, being known only as a rarity in Brazilian Guiana and the Amazons. The following specimens are in the collection of the British Museum: Brazil, type ♀ (*F. Smith* coll.); BRITISH GUIANA: Essequibo R., Moraballi Creek, on trail, 25.ix. and 7.xi.1929, 2 ♀ (*Oxford Univ. Exped.*).

The species is allied to *P. traili* Cameron, 1906 (= *P. vjhelyii* Ducke, 1910 var. *obscura* Ducke, 1910, **syn. n.**) sharing the following characters with it: occiput distinctly emarginate, pronotum with no fovea, with the keel developed only laterally, not in the centre, and with the anterior margin rather strongly lamellate. It differs in its shorter, more rounded clypeus and much shorter 1st abdominal segment. It would run to *P. vjhelyii* in Bequaert's key (1944: 277). In neither species is anything known of the nest.

6. *Polybia bifasciata* Saussure, 1854.

Bequaert (1944: 283) records the typical variety from BRITISH GUIANA: Kartabo and Demerara R., and the var. *quadricincta* Saussure, 1854, from

Bartica, Kartabo, Source of Essequibo R., Warina and N.W. District. The following specimens are in the collection of the British Museum: var. *bifasciata* Sauss., Mazaruni Station, on window of colony house, 16.ix. and 19.ix.1937, 2 ♀ (*Richards and Smart*); var. *quadricincta* Sauss., Mazaruni Station, on window of colony house, 26.viii. and 16.ix.1937, 2 ♀ (*Richards and Smart*); no precise locality, 2 ♀.

From a nest (no. 251) Essequibo R., Moraballi Creek, 14.viii.1929 (*Oxford Univ. Exped.*), 9 ♀ were preserved, 4 of the typical form and 5 of the var. *quadricincta*.

Under various forms the species is known from Mexico to S. Brazil. The nest has been figured by Dücke (1905b: pl. 3, fig. 13). It is ovoid, with excentric exit-hole, rather solid envelope and not many combs.

7. *Polybia sericea* (Olivier, 1791).

As pointed out by Bequaert (1944: 284), who recorded the species from BRITISH GUIANA: Georgetown, Demerara, Onverwagt, Bartica district and Mt. Roraima, the Guiana specimens all belong to the var. *nigripennis* (Fabricius [1805]) (= *Polybia nigriceps* Cameron, 1912, *syn. n.*) in which the 2nd as well as the 1st abdominal segment is reddish. In the British Museum collection 1 ♂, 12 ♀ from British Guiana all belong to the variety, whereas 9 ♂, 56 ♀ from other areas belong to the typical form which is found from Guatemala to Argentina. In British Guiana the species seems to be much commoner on the coastal plain than inland. According to H. von Ihering (1896a: 451) it stores a certain amount of honey. The nest has been described by de Saussure (1854: pl. 29, figs. 1-3), Möbius (1856: pl. iii) Brèthes (1902: pl. viii, figs. 3 and 4) and Strand (1912: 318). It is like that of *P. occidentalis* (Oliv.) (p. 43) but larger. The one figured by Brèthes was elongate-cylindrical, 36.0 × 18.0 cm., and had 11 combs.

The adult wasps are closely resembled in colour by the following insects: *Polistes subsericeus* Sauss., *Montezumia brunnea* Sauss., *M. infernalis* Spin., *Pachymenes sericeus* Sauss. (VESPIDAE), *Pseudosphex polybioides* Burm. (Lep., SYNTOMIDAE), *Odyneropsis holosericea* Schrtk. (Apoidea), *Sphecomorpha* sp. (Col.) (Dücke, 1910: 460; Bertoni, 1911; Schrottky, 1915).

8. *Polybia chrysothorax* (Weber, 1801).

Recorded from British Guiana by Cameron (1912), Bodkin (1917) and Bequaert (1944: 284), it seems to be common on the more open areas, especially on the coastal plain.

The nest has been described by de Saussure (1858: cvii) but does not seem to have been figured. Poulton (1932) recorded that it was closely resembled in colour by a Syntomid moth, *Pseudosphex ? klagesii* Rothschild.

9. *Polybia micans* Dücke, 1904.

This species was described from British Guiana as *P. sericeibalteata* Cameron, 1912 (type, ♀, in coll. B.M.), and recorded (as *P. velutina* Dücke) by Bodkin (1917) from North-west district, Issororo (♀, vii.1916 (*C. B. Williams*) in coll. B.M.). It is recorded by Bequaert (1944: 294) from Kartabo and Bartica. There are 3 females in the British Museum collection from R.

Mazaruni, Tituba, xi.1916 (*G. E. Bodkin*) and in coll., Dept. Agric., Berbice R., Takano Creek, ii.1919, ♂ (*A. A. Abrahams*); Potaro R., Tumatumari, xii.1915, ♀ (*G. E. Bodkin*).

The true var. *velutina* Ducke, 1907 is recorded by Bequaert from Arakaka, and there is a specimen in coll. Dept. Agric., N.W. District, vi.1915, ♀ (*G. E. Bodkin*). The species as a whole is found from Colombia to Peru, Bolivia and Amazonia.

According to Ducke (1910:505), the nest of the typical form is ovoid, like that of many other species of the genus. The same author found a nest of the var. *velutina* (1 ♀, in coll. B.M.) on the Rio Japurá. It was on a tree near an ants' nest whose irregular rounded shape it seemed to imitate.

We found one nest, no. 353, of the typical form, firmly attached to the twig of a small tree, 3 ft. from the ground, in high forest on the edge of a teak plantation, Mazaruni Station, 28.ix.1937. The envelope was brown and crumbly, not fibrous, but with many elongate particles. The cells were 5.0×17.0 mm., and the cocoons were slightly domed but not projecting. There were 3 combs and possibly a small disused one at the top. All the cells had been used before and contained eggs, larvae and cocoons, scattered more or less at random. There were 197 wasps and another 6-10 were probably lost. The wasps consisted of 40 males, 1 queen (22 eggs), 28 intermediates with rather well-developed, 13 with less well-developed ovaries, and 115 workers. This was evidently a colony in a late stage of development, and the intermediates may well have been young queens. The contents of the combs were as follows: top, 116 cells, 25 cocoons; second, 172 cells, 50 cocoons; bottom, 165 cells, 29 cocoons. Total, 453 cells, 194 cocoons and approximately 175 larvae and 174 eggs. The age of the nest was probably about 2:40; egg/♀ ratio = 174; cell/wasp ratio = 2.9; larva/worker ratio = 1.1; egg/ovarial egg ratio = 7.9.

10. *Polybia affinis* du Buysson, 1908.

This species has not previously been recorded from British Guiana, but we have seen the following specimens: FRENCH GUIANA: Saint-Laurent du Maroni, ♀ (det. A. Ducke); BRITISH GUIANA: Potaro River, Kaieteur Savannah, Potaro trail, 5.ix., 1 ♀, Takeit trail, 9.ix., 1 ♀, Savannah, 10.ix.1937, 1 ♀ (*Richards* and *Smart*); Essequibo R., Moraballi Creek, dark forest, 27.ix.1929, 1 ♀ (*Oxford Univ. Exped.*); Berbice R., Takama Creek, ii.1919, 3 ♀ (*A. A. Abrahams*).

The species is very close to *P. micans* Ducke to which it would run in Bequaert's key (1944), but the abdomen is a little more sericeous, and the propodeal furrow has its sides somewhat less raised and tends not to extend so far upwards. The specimens correspond to the paler forms mentioned by Ducke (1910:504) and have a considerable resemblance to *Synoeca virginea* (Fab.).

11. *Polybia dimidiata* (Olivier, 1791).

This distinct and well-known species is widespread in British Guiana. It was recorded by Cameron (1912) and by Bodkin (1917) from Rockstone on the Essequibo. Bequaert (1944:285) gives West bank of Demerara R.; Oronoque R., 2° 42' N.; Mazaruni Station (= Penal Settlement). We have

seen the following specimens : Mazaruni Station, clearing, on flowers of *Cassia*, 18. ix. 1937, 1 ♀ ; Cuyuni R., Kamaria landing, 21. xi. 1929, 1 ♀ (*Oxford Univ. Exped.*) ; Kuruabaru Creek, ix. 1919, 3 ♀ (*A. A. Abrahams*, Dept. Agric.) ; no precise locality, 4 ♀ (*J. Rodway*, *A. W. Bartlett*, *P. Cameron* coll.).

Elsewhere the species is known from Colombia to Peru, Bolivia and S. Brazil. According to Ducke (1910 : 506, fig. 8) the nests are very large, of a cylindrical shape, becoming conical at the top. They are always built round a branch, which pierces all the combs. The envelope is brown, coarse but pliable, and the exit-hole is excentric. The one he figures has 20 combs, and must have been of considerable age, it was 80 cm. long. R. von Ihering (1904 : 259, pl. 7, fig. 17) describes one 57 cm. long and 37 cm. in diameter near the bottom ; this had 17 combs, and in the upper combs the bottom of the cells contained a thick layer of dried larval faeces, showing that they had been used more than once. In another nest of 11 combs no such layer of faeces was seen. According to this author (p. 286), the queen is smaller than the worker in this species. At São Paulo he bred from the nest the Trigonalid parasite, *Nomadina cisandina* Schulz (Schulz, 1905 : 93). The following insects more or less closely resemble *P. dimidiata* in colour : *Polistes bicolor* Ducke, *P. occipitalis* Ducke, *P. erythrogaster* Ducke, *Montezumia infundibuliformis* Sauss., *M. difficilis* Ducke, *Nortonia* [*Parazumia*] *carinulata* (Spin.) (VESPIDAE) ; *Cerioides braueri* Williston (SYRPHIDAE) (Schulz, 1905 : 114 ; Ducke, 1910 : 460 ; Bequaert, 1944 : 285).

12. *Polybia rejecta* (Fabricius, 1798).

This wasp is common in British Guiana, and has been recorded by Cameron (1912), Bodkin (1917) and Bequaert (1944 : 285) from a number of localities. Myers (1929 ; 1935) gives a number of records of the colonies being associated, in British Guiana, with Dolichoderine ants and with birds' nests (see p. 99).

The typical form of the species is chiefly found in Trinidad, the Guianas and Amazonia, but the complete range extends from Mexico to Peru and S. Brazil.

The nest has various shapes, from spherical to cylindrical or more or less conical (broad end downwards). Good illustrations have been published by de Saussure (1854 : pl. 29, figs. 4-6), Moebius (1856 : pl. 4), and FitzGerald (1938 : pl. 3, fig. 8). The last-named figure shows the close proximity to the nests of the ant, *Azteca* (DOLICHODERINAE). FitzGerald also records as enemies of *P. rejecta* in Trinidad, the Asilid fly, *Nusa erythropyga* Wied., and a Tachinid parasite of the larva, *Telothyriosoma polybia* Curran. Some notes on the nest are also given by R. von Ihering (1904 : 261). For a figure of the interior, see pl. 2, fig. 15.

In 1937 a number of nests was found on one mango tree in the clearing at Mazaruni Station (pl. 2, figs. 13 and 14). The tree had several large cartons (possibly parts of one colony) of the ant *Dolichoderus* (*Hypoclinea*) *bidens* (L.) (det. Donisthorpe), which swarmed all over the trunk and branches. There were at least 8 nests of *P. rejecta* of varying size, at points 25-40 ft. above the ground. At the tip of a branch, 15 ft. from the ground, and at the same distance from the nearest *Polybia* nest, were 4 or 5 old hanging nests of the Oriole, *Cassicus cela* Linn. There was also an occupied nest of *Pachyrrhamphus rufus* Boddaert (COTINGIDAE) (det. T. A. W. Davis). The same tree bore the

following nests of other Aculeate Hymenoptera: *Mischocyttarus injucundus bimarginatus* (Cam.) 3 (the only ones seen at Mazaruni), *M. cerberus acheron* Rich. 2, *Protopolybia minutissima* (Spin.) 1, *Metapolybia cingulata* (Fab.) 1, *Trypoxylon nitidum* Sm. 1, *Sceliphron fistulare* (Dahlb.) 3 [deserted]. The close resemblance in colour between the adults of *Mischocyttarus injucundus* and those of *P. rejecta* has already been noted by FitzGerald (1939: 105) in Trinidad.

It is highly probable that *P. rejecta* had long occupied this tree, and that new colonies had budded off the original ones. The ants made climbing on the tree very unpleasant, and the wasps must in some way have come to terms with them.

Since the *Polybia* nests were large and broadly attached to thick branches, it was extremely difficult to capture them whole. This was attempted, without much success, by using a net on a very long pole. Many wasps escaped, but a number of these formed swarms near the nest-site and were captured later. Three nests were partially studied. The envelopes were greyish-brown, slightly more fibrous than in *P. occidentalis*, but thick and crumbly. The cells were 9.0×3.5 mm., and the cocoons projected 3.5 mm. beyond the rims of the cells.

Nest 82, taken on 22.viii., was 22.5 cm. long and about 12.5 cm. diameter, but narrowing considerably to the point of attachment. At the first attempt 224 wasps and the nest were captured, but the majority of wasps escaped. Later, these formed two swarms, one low down on a leaf and another smaller one on a branch just above the original site. The lower swarm was captured almost entire and consisted of 753 wasps, so 977 wasps were caught of a total of, perhaps, 1400.

At the time 150 wasps were dissected. All these were workers with ovarioles sometimes filamentous, sometimes with more obvious rudiments, but never of the intermediate type in which a few eggs are clearly larger than the other rudiments. Twelve of the workers contained Gregarines of the long and round types. In London another 250 wasps were dissected from alcohol, and one queen with 63 eggs in her ovaries was found amongst them.

The nest contained 9 combs; the number of cells and their contents are shown in Table 7; the cells of the top 7 combs had all been used before.

TABLE 7.

Polybia rejecta (Fab.), nest 82, contents of nest.

Comb no.	No. of cells	Contents
Top	680	Mainly cocoons, a few old larvae, eggs and young larvae at edges.
2nd	900	Mainly cocoons, a few old larvae in middle and at edges
3rd	1040	Mainly cocoons, a few young larvae and eggs at edges.
4th	1664	Many cocoons and old larvae, fewer young larvae and eggs.
5th	880	Many cocoons and old larvae, some young larvae, few eggs.
6th	652	Mainly cocoons and old larvae.
7th	700	Mainly eggs and young larvae, some old larvae and cocoons.
8th	640	Mainly empty, about 100 cocoons.
9th	602	Shallow, empty cells.
Total	7758	(Estimated) 3500 cocoons, 2400 larvae, 800 eggs.

Assuming that there were 1400 inhabitants, the cell/wasp ratio was 5.54, and the larva/worker ratio 1.7. It is impossible to guess the age of the nest; it seems likely that the colonies of this species are much more permanent than those of *P. occidentalis* (Oliv.), etc., perhaps lasting some years and budding off several new colonies before disintegrating.

Nest 132, on the same tree, was taken on 28.viii. It broke in the process and almost all the wasps were lost. A swarm, estimated to be of 200-300 wasps, formed on the old nest-site, but could not be captured. The nest was approximately $12.5 \times 18.0 \times 7.5$ cm., and contained at least 3, and possibly 4, combs. Of the 14 wasps dissected, all were workers and 7 contained round Gregarines in the body-cavity.

Nest 309, on the same tree, taken 23.ix. This was a rather large nest, approximately $30.0 \times 12.5 \times 10.0$ cm., on a branch about 30 ft. above the ground. 1780 wasps were captured, but about 1000 were lost and formed a dense swarm at the old nest-site. They were still there on the next morning but had disappeared by 5.30 p.m. 350 wasps were dissected, and 12 queens and 338 workers were recognised. The queens had 7, 8, 10, 11, 13 (2), 14 (2), 17 and 22 (2) eggs (mean 13.5) in their ovaries; 3 (8, 12, 22 eggs) had elongate Gregarines in the body-cavity. The workers all had filamentous or very slightly developed ovaries, with no approach to the intermediate type. Fifty-three were parasitised by elongate Gregarines and one by round ones. In the dissected workers, two were found to contain Strepsiptera. The whole lot of 1780 was then examined, and 3 ♂, 1 ♀ Strepsiptera (= 0.2 per cent.) were discovered as visible externally (cf. p. 99).

The nest contained 12 combs, of which the contents are shown in Table 8. The numbers of cells and cocoons were counted; those of larvae and eggs have been estimated. The first nine combs and at least the centre of the tenth consisted of cells which had been used before.

TABLE 8.

Polybia rejecta (Fab.), nest 309, contents of nest.

Comb no.	No. of cells	No. of cocoons	No. of larvae	No. of eggs	Arrangement
Top	54	10	44	0	Irregular.
2nd	227	64	163	0	"
3rd	551	170	300	81	"
4th	1184	500	500	184	"
5th	944	217	600	127	Cocoons round edge.
6th	1024	315	600	109	Cocoons in centre.
7th	860	280	500	80	Irregular.
8th	860	288	472	100	"
9th	960	206	600	154	Cocoons round edge.
10th	694	16	178	500	Irregular.
11th	est. 600	0	0	0	Empty, shallow.
12th	est. 500	0	0	0	ditto.
Totals	8458	2066	3957	1335	

Assuming that there were 2780 wasps, the cell/wasp ratio was 3.04 and the larva/worker ratio 1.47. The nest would have contained 96 queens with an average of 13.5 ovarian eggs each. The egg/ovarial egg ratio would therefore have been just over 1.0.

In nest 309 the wing-lengths and hamuli-numbers were recorded in 27 queens¹³ and 40 workers, but there was no significant difference: wing-lengths, ♀ 9.05, ♂ 9.10 mm.; hamuli, ♀ 7.1, ♂ 7.3.

Five other characters were also measured with a screw eye-piece micro-meter in 10 ♀ and 10 ♂; these all differed significantly, and the results are shown in Table 9.

TABLE 9.

Comparisons of mean measurements (mm.) of 10 queens and 10 workers of *Polybia rejecta* (Fab.), from nest 309. The differences are taken as significant when $P < 0.05$.

Character/ caste	Minimum width of vertex	Length of mesonotum	Length of abdominal tergite 1		Width of tergite 1 at posterior margin.
			(a) Dorsal muscle to divergence of sides	(b) Diver- gence of sides to posterior margin	
♀	1.544	2.163	0.373	1.531	1.333
♂	1.578	2.224	0.444	1.406	1.270
Value of P	< .05	< .05	< .01	< .01	< .01

The most significant difference is in the shape of the 1st abdominal tergite. In the queens this starts diverging earlier and has a broader posterior margin. The difference in the mean *total* length of the segment, ♀ 1.904, ♂ 1.850 mm., is not significant. This enlargement of the petiole in the queen seems to be similar to that described in *Stelopolybia vicina* (Sauss.) by R. von Ihering (1903a).

13. *Polybia occidentalis* (Olivier, 1791).

It is shown in Appendix 1 (p. 140) that this species occurs in British Guiana in three subspecies, subsp. *cincta* (Provancher), subsp. *platycephala* Rich., and what will for the moment be called the typical subspecies. The first-named is confined to the coastal plain and is the same as the form found in Trinidad. The second is the usual form in most of the Guiana rain-forest area, and most of our observations were made on it. One nest of the last-named subspecies, which has a Brazilian distribution, was studied on the Kaieteur Savannah. Owing to the confused state of the taxonomy of the group, only a few of the more important references to the earlier literature will be quoted. Ducke's account (1910), for instance, includes under the name "*occidentalis*" what are here treated as four species with their subspecies.

(a) Subsp. *platycephala* Richards.

Ten nests were found and of these, five were more or less fully investigated. Four other deserted nests, inhabited by ants, probably belonged to this species.

¹³ Some additional queens were picked out of the preserved material.

The initial number of combs appears to be two or three, but eventually as many as seven combs may be constructed, so that the shape of the nest changes from an ovoid to a cylinder with rounded ends. The dimensions of four nests are shown in Table 10.

The nest is attached to a large leaf or to the twig of a tree, either in open places or in relatively open second-growth forest. It would seem that in high forest it is mainly found on the banks of creeks where some sun can penetrate. The nest itself is placed so as to be sheltered from the sun in the middle of the day, as is found as soon as one attempts to take a photograph (the best time for this seemed to be about 9.0 a.m.).

TABLE 10.

Dimensions of four nests of *Polybia occidentalis platycephala* Rich.

Nest no.	No. of combs	Vertical length, cm.	Approximate diameter, cm.
34	3	6.0	4.5-5.5
275	3	6.0	pyriform
10	5	9.5	6.0
310	6	15.0	

The entrance-hole is below the lowest comb but on one side of the envelope, well above its lowest point. The intercommunicating holes between the combs are also usually on one side and about 5.0 mm. in diameter. The envelope is streaky brown or grey, not fibrous, but brittle and made of small pieces of vegetable material stuck together side by side. Typically, the cells are 2.5-2.7 mm. wide and 6.0 mm. deep. The white cocoons project strongly below the rim of the cell, by 3.5 mm. Nest 26 differed rather widely from these figures; the cells were shallow and only 2.25 mm. wide. This nest had apparently only been made a few days, and the cells would presumably have been broader when they reached their full length. Nests 34, 105, 275 and 310 were predominantly brown; nests 10, 26 and 314 grey. In nest 314 the envelope had pronounced dark streaks formed by shining black particles. Two nests, numbers 10 and 34, contained a number of more or less dismembered winged termites. In Table 11 the nests are arranged in estimated order of age. In the account below, five best investigated nests are dealt with first, then five others on which some observations were made; finally, the four which had been invaded by ants are listed.

Nest 26, Mazaruni Station, clearing, on small twig of *Citrus*, 7 ft. from ground, 15.viii. The wasps were quite normal in appearance and were, if anything, rather large, wing-lengths of ♀ and ♂ being 7.5-8.0 mm. The cells were abnormally small, 2.25 mm. in diameter. As they were very shallow and empty, it is probable that the whole nest had just been built and that the cells would have reached the normal diameter when completed. The nest was first seen on 14.viii., and the lower part of the envelope was then absent but it was almost complete on 15.viii. The nest was attached to the tip by a small comb of ten cells (? the remains of an earlier nest) which was shut off in a small chamber. Below were two combs of 113 and 191 very

shallow, empty cells. In the 128 workers which were dissected, about 10 appeared to have the hind-gut full of meconium, improbable as this sounds. Two had 3-4 Gregarines in the body-cavity and one had an elongate Gregarine in the gut. Two had Strepsipterous larvae in the body-cavity. The presence of the meconium in the gut of some workers, together with other features of the nest, suggest that it was really a secondary one formed after the destruction of an earlier one which had already reached an age of 1.0 +. This is supported by the very high average number (27.0) of ovarial eggs in the queens, which would not be expected in a young nest.

Nest 34, Mazaruni Station, clearing, on twig of large tree, 8 ft. from ground, 17.viii. There were three combs, the two top ones nearly circular, the bottom one oval. Four dealate and one winged termite were found in the nest. Of the 98 workers dissected, 15 contained Gregarines in the fore-gut, 13 of an elongate kind, one of a large circular kind, and one of a bilobed kind.

Nest 275, Mazaruni Station, second-growth forest, on twig of a mango tree, 6 ft. from ground, 18.ix. There were three combs, the top one containing only eggs, the other two eggs larvae and each one cocoon. Some of the cells in the bottom comb were still incomplete. It seemed that there were the three original combs and that the first-laid eggs were approaching the end of their development. Of the 78 workers dissected, 26 had Gregarines in the body-cavity.

Nest 105, Mazaruni Station, clearing, on a twig of mango tree, 20 ft. from ground, 25.viii. There were four combs and nine cells of a new comb had been started at the bottom of the outside of the envelope. The top two combs were of cells being used a second time, the bottom two were not. The third comb contained only eggs, and the bottom one was of empty, shallow cells. Probably this was originally a two-comb nest, but with the hatching of additional workers, two new combs, and the beginning of the third, had been constructed. Of the 96 workers dissected, only one contained Gregarines. It was noticed in these workers that the spermatheca was quite easily seen and not much smaller than that of the queens.

Nest 310, Mazaruni Station, clearing, on twig of small *Citrus* bush, 8 ft. from ground, 24.ix. (pl. 2, figs. 16 and 17). There were six combs, the cells of the top three having been used before, those of the bottom three being used for the first time. The two bottom combs were empty, and the cells of the lowest one were still quite shallow. This nest was taken on one of the last days of our stay, and no wasps were dissected until 1946.

Nest 10, Mazaruni Station, clearing, on twig of *Citrus*, 5 ft. from ground, 11.viii. (pl. 2, fig. 18). Nearly all the wasps were lost in trying to take the nest whole; three days later a few males emerged from the combs, so the nest was probably in a late stage in its development. It contained a large number of termites, mostly dealated or even more chopped up; only a few were whole and winged. The five combs were not examined until later, but a partial record of their contents is given in Table 11.

The next five nests were only partially investigated, but they provide further information on certain points.

Nest 108, Mazaruni Station, clearing, nest in small *Citrus*, 25.viii. This was broken in removing it from the tree and most of the wasps were lost; 133 were captured and all of these were workers, 3 containing Gregarines.

There were seven combs of 65 (top), 116, 378, 378, 512, 440 (approx.), and 384 (approx.) cells, 2273 in all. They contained 0, 16, 31, 61, 148, 146 and 98 cocoons, respectively, so it was in a fairly advanced state of development.

Nest 301, Mazaruni Station, on twig of small shrub in garden, 4 ft. from ground, 22.ix. The nest was taken at 3.0 p.m., but was much broken; there were apparently 4-5 combs but the cells were not counted. One of the lower combs consisted of shallow cells with eggs only. At least the two upper ones consisted of cells which had been used before and now contained many eggs and larvae and a few cocoons. 366 wasps were taken, and when the site was revisited at 6.30 p.m. no more wasps were found, so presumably the whole colony had been captured. 100 wasps were dissected, and 15 per cent. were queens containing 4-6 eggs.

Nest 314, Mazaruni Station, clearing, on underside of much-divided leaf of palm, 10 ft. from ground, 24.ix. 1227 wasps were taken, apparently not more than 4 being lost, but the nest was not broken up. 100 wasps were dissected, and consisted of 96 ♀ (16 containing Gregarines), 2 ♂, 1 intermediate (2 eggs) and 1 queen (14 eggs).

Nest 339, Mazaruni Station, second-growth forest, on a liane, 25 ft. from ground, 26.ix. The nest was pear-shaped, 6 cm. long, but it was not broken up. 143 were captured, but about an equal number was lost. 100 were dissected, and consisted of 22 queens (3-7 eggs each, average 5.0) and 78 ♀, of which 2 contained Strepsiptera.

Another nest, no. 317, was seen on the leaf of the giant *Cyperus* (*Diplasia karatifolia* Rich.), in second-growth forest, Mazaruni Station, 24.ix., but it was not investigated.

Finally, there are five records of the relations of this species with ants.

Nest 52, Mazaruni Station, clearing, on *Citrus*, 19.viii. This probably belonged to the present subspecies but was occupied by ants, *Camponotus abdominalis* (Fab.) (det. Donisthorpe). Nest 276, with the same data, but seen on 18.ix., was inhabited by unidentified ants.

Nest 282, Mazaruni Station, clearing, on *Citrus*, 19.ix., was probably of this subspecies and was inhabited by the ant *Iridomyrmex mazaruni* Donisth. (Donisthorpe, 1939). Another *Citrus*, which contained a nest of *P. occiaentalis*, was found to have ants also, nesting between the leaves. There were *Cremastogaster brevispina* Mayr. (det. Donisthorpe). On one occasion a band of driver ants (*Eciton* sp.) was seen marching (second-growth forest, Mazaruni, ix) carrying the remains of what was almost certainly this species. The fragments of late pupae were fairly easily recognisable.

In *P. occiaentalis* the worker differs slightly from the queen in characters other than ovarian development. The question has been studied in some detail because of the abundant material available and of its theoretical importance. If the workers differ from queens in skeletal structures, it is highly probable that they are in some way treated differently during development.

In a preliminary study the colour-patterns, nine linear measurements, and the number of hamuli on the hind-wings were compared in 17 ♀ and 16 ♂ from 8 different nests. There was no difference in colour-pattern nor in the following measurements; though the queens were always larger, the differences were not significant: width of vertex, three sectors of veins in the fore-

TABLE 11.
Nest data for *Polybia occidentalis* (Oliv.) subsp. *platycephala* Rich.

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Intern.	Eggs	♂	♀	♂	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♀ + Intern.	Eggs/ queens	Eggs/ ovarial eggs
26	113	132	50-70	4	18-42, 27.0	0		128	0	0	0	0	0	304	0	2.3	0	0	0
	191																		
275	304																		
	97	89	4	11	3-7, 3.7	0		78	0	0	1	16	80	0	0.60	3.8	1.2	21.8	5.9
34	138										1	56	80	0					
	99										1	19	80	0					
334											3	91	240	0					
34	204	159	30-40	11	8-12, 9.4	3	5-6	145	0	0	0	0	0	204	0.63	4.2	0.3	35.2	3.7
	285										30	0	255	0					
665	176										0	44	182	0					
105											30	44	387	204					
105	139	215	4-6	9	12-14, 12.75	0		206	0	0	2	37	100	0	1.10	3.8	0.4	57.9	4.5
	250										20	50	180	0					
817	241										0	0	241	187					
	187										0	0	0						
310																			
310	196	596	775	48	4-11, 5.4	0		548	0	0	22	87	521	187	1.43*	3.2	0.7	14.4	2.7
	353										160	18	18	0					
10	416										84	160	109	0					
	412										0	200	216	0					
1915	375										0	0	350	62					
	163										0	0	0	163					
1915											0	0	0	0					
											0	0	0	0					
10	1915										244	378	693	600					
10	193	?	?								10	?	?	?	?				
	246										112	?	?	?	2.0				
1119	326										90	?	?	?					
	194										0	0	194	0					
1119	215										0	0	215	0					
											0	0	0	0					
1119											212		409						

* From top two combs.

wing, length of hind tibia, length of tergite 1 from dorsal muscle-exit to point where the sides begin to diverge. In the following characters significant differences were found: (a) length of mesonotum along mid-line, ♀ mean 1.62, ♂ 1.50 mm. $P < 0.01$; (b) abdominal tergite 1, distance from point where sides start diverging to posterior margin, ♀ mean 1.19, ♂ 1.06 mm., $P < 0.01$; (c) abdominal tergite 1, width at posterior margin, ♀ mean 0.88, ♂ 0.77 mm., $P < 0.01$; (d) number of hamuli, which had the following frequencies:—

	No. of hooks			
	5.	6.	7.	8.
♀	4	7	6	0
♂	0	4	10	2

The three measurements which differed significantly might indicate no more than that the queen was larger than the worker, though the abdominal characters agree with what was found in *P. rejecta* (Fab.). The difference in the number of hamuli, however, is of special interest because there are more in the worker although that caste is the smaller. In Aculeates in general, hamuli-number is positively correlated with size (see p. 110).

In a more extended study of the castes only wing-length and hamuli-number were studied. They were recorded in 55 queens and 234 workers from six nests, and the results are shown in Table 12, the nests being arranged in order of mean worker wing-length.

TABLE 12.

Mean wing-length (mm.) and hamuli-number in ♀ and ♂ from six nests. Columns 3 and 7 give the numbers measured.

Nest no.	Age	Workers				Queens			
		No.	Wing-length	Hamuli-number	Hamuli-per mm.	No.	Wing-length	Hamuli-number	Hamuli-per mm.
339	1.00*	30	7.83	6.77	.86	22	8.18	6.68	.82
34†	0.17	30	7.77	7.03	.90	7	8.00	7.14	.89
26	0.00	30	7.70	7.26	.94	4	7.88	5.75	.73
310	1.32	40	7.65	7.28	.95	8	7.94	7.25	.91
275†	0.21	74	7.55	7.00	.93	8	7.88	7.13	.90
105	1.17	30	7.37	6.80	.92	5	7.40	6.40	.86

* Age of nest estimated from its size and from the number of inhabitants.

† In these two nests the mean hamuli-number is less in the workers than in the queens, though in all nests the workers have more hamuli per mm. wing-length.

Of the 54 queens, the presence of sperm was verified in 24 (four nests); the others were classed as queens from the number of eggs in their ovaries. Young, unfertilised queens would probably be indistinguishable from workers, but none of the nests was old enough for young queens to be present. Taking all the nests together, the mean figures are:—

Caste	No. measured	Wing-length (mm.)	Hook number
♀	54	8.00	6.80
♂	234	7.63	7.03

Examining Table 12, the following conclusions may be drawn:—

(1) The mean wing-lengths of queens and workers are strongly correlated; the hook-numbers are not. The correlation coefficients are $r = +0.9406$ ($P < 0.01$) and $r = -0.03$, respectively.

(2) The mean wing-length of the queens is always greater than that of the corresponding workers. The sum of the differences between the means for each pair is significantly greater than zero ($P < 0.01$).

(3) In mean hook-number, the workers exceed the queen in only 4 out of 6 nests. Moreover, the sum of the differences between the means for each pair is not significantly greater than zero.

(4) If a figure is obtained for the number of hooks per millimetre wing-length, then this figure is in all nests greater in the worker than in the queen, but the sum of the differences between these ratios is not significantly greater than zero.

(5) From the original data (54 ♀, 234 ♂), the regressions of hamuli-number on wing-length were calculated. The regression coefficient in the queens was -0.2148 , but this was not significant. In the workers the coefficient was $+0.2496$ (P between 0.05 and 0.02). Thus, in the queens, hook-number is not significantly related to wing-length, whereas in the workers there is a slight but probably significant tendency for the longer-winged workers to have more hooks.

To sum up, then, in this subspecies of *P. occidentalis*, queens tend to be larger than the workers, with longer wings, longer mesonotum, larger distal part of the 1st abdominal segment, but with fewer hamuli for their size. These differences must arise before the wasps leave their pupae, whereas differences in ovarian development might be produced later.

(b) Subsp. *occidentalis* (Oliv.).

For the moment it is convenient to use this name for the form of the species found on the Kaieteur Savannah. It does not seem to differ significantly from the forms found from the Amazon basin to S. Brazil. Only one nest has been fully investigated.

Nest 155, Kaieteur Savannah, beneath leaf of the Bromeliad, *Brocchinia micrantha* (Baker) Mer, 8 ft. from ground, 2.ix. The nest was abnormally placed, perhaps because the leaf had bent down after it was constructed. It was broadly attached to the leaf, with the combs at right angles to the leaf-surface (*i.e.* the long axis of the cells nearly horizontal), and the exit-hole directed horizontally, towards the centre of the plant. The envelope was grey and rather shining. There were four combs. The top one (*i.e.* the furthest from the exit), of 43 cells, was probably disused; the second, of 231 cells, was apparently empty; the third, of 480 cells, contained 33 cocoons but most of the rest were empty; the bottom comb, of 455 cells, contained 5 cocoons but was mostly empty. There was a small quantity of honey in a few cells. It would appear that this nest had about completed its cycle, and was about to disperse. The wasps were dissected after preservation in alcohol, so sperm was not found, but it is possible that the "intermediates" were young queens corresponding to the males. The characters of queens (7), intermediates (6), and workers (7) were recorded for taxonomic study (Appendix, p. 135). The differences were mostly small and not significant (width of vertex, POL: OOL

ratio, eye/tempora ratio, 1st tergite ratio, width of tergite 1). The length of tergite 1 did, however, differ significantly between workers and queens (P between 0.02 and 0.01): length of queens 1.572, intermediates 1.495, workers 1.508 mm. The length of the fore-wing and the number of hooks on the hind-wing were recorded in 9 queens, 12 intermediates and 54 workers, with the following results (Table 13).

TABLE 13.

Length of fore-wing (mm.) and hamuli-number in 9 ♀, 12 intermediates and 54 workers of *Polybia o. occidentalis* (Oliv.), nest 155.

	Length of fore-wing			Number of hamuli			
	7.0	7.5	Mean	6	7	8	Mean
Queen . . .	5	4	7.22	3	4	2	6.89
Intermediate	6	6	7.25	1	8	3	7.17
Worker . . .	40	14	7.13	8	34	12	7.07

The difference between the number of hamuli in the queens and workers is probably significant (P between 0.05 and 0.02), but the castes, in this nest, are poorly differentiated; the intermediates seem to be more like workers than queens. The complete data for the nest are summarised in Table 14.

TABLE 14.

Polybia occidentalis subsp. *occidentalis* (Oliv.), data of nest 155.

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	♂	♂
155	43 231 480 455 1209	207	10-20	19	4-13, 10-8	25	109	54

Nest no.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ Wasps
155	0 0 33 5 38	0 0 0 0 0	0 0 0 0 0	43 231 447 450 1171	† 2.0	5.8

This nest differed from those of the subsp. *platycephala* in the large number of intermediates. The cells and cocoons did not seem to differ.

(c) Records of the biology of *Polybia occidentalis* (Oliv.) in the literature.

In giving a summary of literature concerning *P. occidentalis*, it is convenient to treat all forms together, since it is often difficult, or impossible, to tell which of them was being observed.

Bodkin (1907 : 307) has some notes on the biology of what must have been the subsp. *cineta* (Prov.) in British Guiana. He states that it is very common on the coastlands and occasionally met with in the interior (*i.e.* subsp. *platycephala*). The nests are often attached to the leaves of palms. It is one of

the less pugnacious species. The local name of "honey maribunta" suggests that perhaps more honey is stored than is ever the case with subsp. *platycephala* Rich. Large quantities of honey are stored by the var. *scutellaris* (White) (see on) and, according to du Buysson (1910:239), considerable quantities of honey are also stored in Mexico, presumably by the subsp. *nausicaa* Rich. In that country the inhabitants cut most of the nest away to obtain the honey, and the wasps rebuild the nest on the old site. Other records which probably refer to the subsp. *cincta* are the statements of Moore (1913:310), that *P. occidentalis* attacks the sugar-cane Termite, *Eutermes costaricensis* Holmg., in British Guiana; of Williams (1928a:79, footnote), that it attacks the Delphacid, *Neomalaxa flava* Muir, on the underside of the leaves of a succulent grass, in British Guiana; and of FitzGerald (1938:186), that the envelope of the nests in Trinidad often has stalactite-like projections arising from ridges (cf. next record).

One of the detailed studies of a colony of *P. occidentalis* is that made by Schwarz (1931), in Panama (identified as var. *scutellaris* but certainly subsp. *spilonota* Cam. in reality). It appeared that a colony of about 130 wasps was driven from its nest by army ants, and the colony actually studied was the new one which they built nearby. The nest consisted of two combs of 109 and 280 cells respectively. The envelope bore six long, stalactite-like ridges, 7.0-16.0 mm. long. Most of the nest was constructed in 5 days. When observations ceased, after 26 days, there were 20 cocoons and a number of full-grown larvae, but no new wasps had emerged. The cells were 3.0 mm. in diameter, and the cocoons projected about 4.0 mm. beyond the rims of the cells. For many other interesting details, the original paper should be consulted. Further descriptions of colonies in Panama are given by Rau (1933:56), who records that they store large quantities of honey and also capture ants.

Strand (1914) illustrates two nests of what was probably the ordinary Brazilian form (subsp. *occidentalis* (Oliv.)). They seem to have had about six combs and to resemble the British Guiana nests. The account given by Bertoni (1911:118) of the nesting habits of *P. occidentalis* (not the var. *scutellaris*) in Paraguay requires revision when the southern forms of the species are better understood.

The following insects have been recorded as having a marked colour-resemblance to *P. occidentalis* (Oliv.): *Mischocyttarus punctatus* (Ducke), *Eumenes* sp. (VESPIDAE); *Podosesia* sp. (Lep., AEGEIIDAE); *Sphecomorpha murina* Klug (Col.) (Bertoni, 1911:145; Poulton, 1931; FitzGerald, 1939:105).

One of the most difficult problems in the taxonomy of *Polybia occidentalis* concerns the var. *scutellaris* (White). This was described by White (1841), from a nest found on the banks of the R. Nancy, a tributary of the R. Uruguay (see White, 1843), as *Myrapetra scutellaris*. The remarkable spiny envelope, characteristic of the larger nests, is described. Inside the nest were found the remains of much honey, of a Bibionid fly and of a Mantispid, later recorded as *Symphrasia varia* (Walker).¹⁴

¹⁴ For other records of this parasite see F. Smith (1864:501), Westwood (1867:505) and Bruch (1936). We have seen two females of *Symphrasia* sp. (det. D. E. Kimmins) bred from the nest of *Trigonopsis violaceus* Smith (SPHECIDAE), in Trinidad, by Mr. D. Vesey FitzGerald. The nomenclature of the parasite of *P. scutellaris* seems to be very confused.

As shown in the Appendix (p. 147), this form scarcely differs structurally from *P. occidentalis*, though, in the material examined, the colour-pattern was distinct. Other authors, however, claim that intermediates occur both in colour-pattern and in nest-structure (H. von Ihering, 1896; Ducke, 1910: 497; 1914: 323). Von Ihering uses the name var. *paulista* for *scutellaris*-like specimens from smooth nests. Bruch (1936), on the other hand, shows that the young nests of *scutellaris* do not have spines on the envelope, but that they are added in the second year. Bertoni (1911) apparently found two forms in Paraguay; small, smooth nests (= var. *paulista*) and larger, spiny nests, the two occurring in different habitats. We incline to the view that there are really two species: *P. scutellaris* (White), of which the colonies last for several years, building large nests which, after the early stages, have a spiny envelope, and *P. occidentalis* (Oliv.) (form approaching the typical subspecies), of which the colonies are smaller, possibly more ephemeral, and the envelope not spiny, though sometimes with a few larger processes. It is not at all clear to what extent intermediates in colour-pattern are really developed, but the whole question requires reinvestigation, both in the field and in the laboratory.

Bruch (1936), who observed var. *scutellaris* in northern Argentina, states that the nests are founded in the early summer and that by autumn they are 12-15 cm. long, and rather more in diameter. Spines are then just beginning to show on the envelope. In the delta of the Paraná he saw very large old nests 60 cm. long, or more. He was also fortunate enough to see a nest started by a swarm on a tree and to follow its history intermittently for four seasons. A summary of these observations is given in Table 14A.

TABLE 14A.

History of a nest of *P. occidentalis* (Oliv.) var. *scutellaris* (White), after Bruch (1936).

Season	Date	
1st summer	i. 1931	Swarm seen on tree; stayed agglomerated for 4 days.
	15.i. 1931	A convex roof built.
	i-ii. 1931	Six combs built.
	1-14.iv. 1931	Max. diameter 10 cm.; envelope almost smooth.
1st winter	v.-ix. 1931	Hibernated in the nest.
2nd summer	x. 1931	Started making a new nest on another branch, in a less constricted site, using material from old nest. During that summer 7 combs made; max. diam. 18 cm.
	iv. 1932	Strengthening nest and its attachments; much food brought in.
2nd winter	v.-x. 1932	Hibernated in nest.
3rd summer	x. 1932 to spring, 1933	Worked hard, but for some unknown reason several thousand wasps died and were carried out on 3.xii. 1932.
	v. 1933	Nest now 32 cm. long, 26 cm. basal diameter, envelope with many protuberances.
4th summer	x. 1934 to 10.xii. 1934	Three more combs added.
	iii. 1935	Nest found abandoned (reason unknown); apparently about 18 combs.

Lucas (1867, 1885) records very large nests, as much as 1 metre in diameter, which he believed to be up to 25 years old. The observations of Schupp (1896) and Wasmann (1897) show that var. *scutellaris* frequently stores large quantities of deålated, more or less mutilated termites. The same habit is recorded somewhat less frequently in other forms of *P. occidentalis*; Wheeler (1923 : 309-10, as *Protopolybia occidentalis*) records a nest of some form of the species, found by Bradley at Lassance, Minas Geraes, 13.xi.1919, which contained half a pint of deålated termites, while Strand (1912 : 318) records J. D. Anisits observations on the destruction of termites in Paraguay. Bruch (1936) states that the nests of var. *scutellaris* contain, besides honey, a variety of dead insects of all orders, partly chewed up. They are much less purely melliferous than the lechiguana (*Brachygastra lecheguana* Latr.). They catch especially Diptera (Chironomids), winged ants (*Solenopsis* and *Pheidole*), and termites. They also take the case-bearing larvae of *Oecitikus kirbyi* Gould. In summer the larvae are fed on insects only, and little honey is stored; this being the support of the colony during hibernation. Br  thes (1902) also describes the nests of var. *scutellaris* in Argentina and gives a useful bibliographical note. The nests seem commonly to have about 12 combs which contain a quantity of sweet, concentrated honey. Bertoni (1911 : 119, apparently found two forms of the var. *scutellaris* in Paraguay. The form *paulista* H. von Ihering, found over the low bush district of the Alta Parana  , and the ordinary form found in the more open "campos." The first form makes smaller nests which are not spiny; the wasps are said, in the winter, to make spherical nests (4.0 cm. diameter) in which no breeding occurs. The typical form makes larger nests with the characteristic spiny envelope, and stores a quantity of honey. The wasp also catches *Simulium*, which it has been seen to pick off cows. Bertoni suggests that the spines of the envelope may have a protective value. A woodpecker, *Leuconerpes candidus* (Otto), which is a serious enemy of the more fragile type of wasps' nest, is abundant in the campos but absent from the low bush. Other views, as to the possible functions of the spines, are that they are a protection against wild FELIDAE (White, 1841), that they help in insulation and in allowing rain to run off (Bruch, 1936), that they are a protection against low temperatures (H. von Ihering, 1896a), or (very improbable) that there is a protective resemblance to similar-looking termite nests (on the R. Japur  , Ducke, 1906).

Besides *Symphyrasis varia* (Walk.), already mentioned, the following parasites or scavengers in the nests have been recorded: the cockroach, *Sphecophila polybiarum* Shelf. (Shelford, 1906 : 15), which was found in the nests of "*Polybia pygmaea* Fab." in French Guiana. The wasp was probably a form of *P. occidentalis* (Oliv.), and the cockroach is allied to *Attaphila* which lives in the nests of leaf-cutting ants. *Polybiaphila fitzgeraldi* Curran (1917 : 3) was bred from the nest of *P. occidentalis cincta* (Prov.) in Trinidad by D. Vesey Fitzgerald. *Ptinus bruchi* Pic. was found in the nests of the var. *scutellaris* by Bruch (1936).

14. *Polybia parvala* (Fab.)

Polistes parvalus Fabricius [1805].

This name has been used by Bequaert (1944 : 237) for all the forms of *P. occidentalis* (Oliv.) in which the pale markings are much reduced. It is

shown, however, in the Appendix (p. 137) that a small dark wasp exists which differs in structure from the *P. occidentalis* occurring in the same localities. There are also slight differences in nest-biology, and it appears that *P. parvula* is best regarded as a closely allied species. Rare individuals in the nests of *P. occidentalis* may resemble it in colour but the averages of both colour and structure for nest-populations of the two forms are quite different. Two colonies of *P. parvula* were studied in British Guiana.

Nest 85, Mazaruni Station, clearing, on twig of mango, 6 ft. from ground, 23.viii. The wasps were unusually small and dark, and the temporal keel was unusually weak. Apart from their deep black colour and some details of their pale markings, the wasps might almost be called an extreme form of *P. bistrata* (Fab.). The cells were unusually small, only 2.0 mm. wide (2.5-2.7 mm. in *P. occidentalis*). The queens (sperm seen), also, were numerous, with their ovaries not much developed (less than in nest 205, which was apparently younger). The three combs were much broken up in taking the nest, but there were at least 367 cells in all. The top comb contained 5 cocoons, many young and moderate-sized larvae and a few eggs; the second, 19 cocoons, and many eggs and young larvae; the bottom one was of shallow cells, including a large central area of eggs. Of the 98 workers dissected, 16 had round or elongate Gregarines in the gut. One specimen bore the puparium of a male Strepsipteron.

Nest 205, Kaieteur Savannah, beneath twig of small tree by stream, 6 ft. from ground, 5.ix. The wasps were somewhat larger than in nest 85, with the temporal keel somewhat stronger. As in that nest, there was an unusually large number of what were apparently queens (sperm not seen) with poorly developed ovaries (2-5 eggs). The envelope was a flattened spheroid about 5.0 cm. high and 6.2 cm. diameter. There were four combs. The top one, of 34 cells was disused; the second, of 102 cells, full of eggs; the third, of 174 (or more) cells, mostly with eggs but some round the edge empty; the bottom comb of 264 cells, mostly with eggs but the outer ones empty. None of the cells had been used before, so it would appear to have been a young nest. The cells were 2.0 mm. in diameter and 4.0 mm. deep, but had probably not reached their full length. The information about these nests is summarised in Table 15.

The workers seemed to be less differentiated from the queens than in *P. occidentalis*, though in the same direction. In most of the characters measured in the taxonomic study, the castes showed no significant differences; the few that may have some importance are shown in Table 16.

The difference in the value of the 1st tergite ratio is just significant in nest 85 ($P < 0.05$), but not in nest 205.

15. *Polybia bistrata* (Fab.).

There seems to be no proper account of the biology of this species as now restricted. It is common in British Guiana on the east side of the Essequibo R., and occurs in Georgetown; it was also abundant on the Kaieteur Savannah (drainage system of the R. Potaro), but was replaced at Mazaruni Station (west of the Essequibo R.) by *P. bicyttarella* sp. n.

Fifteen complete nests were found in the Potaro valley and five east of the R. Essequibo (Oxford University Exped.). All, except two, consisted of

TABLE 15.
Data of nests of *Polybia parvula* (Fab.).

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	♂	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ 8 + Interm.	Eggs/ queens	Eggs/ ovalal eggs
205	34	858	10	137	2-6, 3-75	0	0	0	0	0	34	0-10	0-7	0	3-4	0-9
	102									102	0					
	174 264									150 220	24 44					
	574									472	102					
85	367 (3 combs)	142	6	28	3-6, 4-6	0	0	24	145	145	53	0-68	2-6	1-8	5-2	1-2

TABLE 16.
Differences between females and workers of *P. parvula* (Fab.). Ranges and means of measurements.

Nest number	Numbers measured	Length of fore-wing (mm.)	Number of hooks on hind-wing	Length of tergite 1 (mm.)	Width of end tergite 1 (mm.)	Tergite 1 ratio, breadth : length
85	8 ♀	6-5-7-5, 6-94	6-7, 6-75	1-27-1-43, 1-36	79-86, 83	567-674, 610
205	8 ♂	6-5-7-0, 6-81	7-8, 7-13	1-33-1-50, 1-40	73-84, 80	539-608, 572
	10 ♀	6-5-7-5, 7-00	7-8, 7-10	1-40-1-54, 1-47	74-89, 84	533-607, 574
	10 ♂	6-5-7-0, 6-65	6-8, 6-80	1-32-1-42, 1-36	71-81, 77	528-599, 565

a single comb only, a flattened ovoid attached by a broad stalk to the underside of a leaf. The entrance was a small circular hole in the centre of the underside of the envelope. Nest 210 had a second comb extending half way across, beneath the top one, itself not enclosed but reaching the entrance-hole to the upper comb. Nest 167 was found deserted (Tukeit-Kaieieur trail, 3.ix.1937), but certainly belonged to this species. It also had two combs, the lower one extending as far as the entrance to the upper one. Both were completely enclosed, and each had its own entrance; the upper one in the centre of its envelope, the lower one at the side of its envelope, near the other entrance. Such an arrangement is unique in the genus *Polybia* and is a departure from the perfect phragmocyttaous type which is diagnostic of the genus, according to Ducke (1910).

The envelope and comb in this species were brownish-grey with white streaks, composed of small pieces of vegetable material (not fibrous), of a crumbly texture. The cells were about 8.0 mm. deep. The width of 12 cells from four nests were measured with a micrometer with the following results: min. 2.50, mean 2.65 ± 0.125 , max. 2.93 mm. The cocoon caps were attached to the rims of the cells and domed up to project 1.0-2.0 mm. above them. Thus there is a significant difference in size of cell from *P. bicyttarella* sp. n. The latter species, though a little larger, has smaller cells but makes up for this by having more projecting cocoons. The wing length of *P. bistrata* is about 0.5 mm. less than that of *P. bicyttarella*. In the following account the nests are described in order of age, the youngest first, and the data are summarised in Table 17.

Nest 166, Tukeit-Kaieieur trail, beneath leaf of Aroid, 3 ft. from ground, 3.ix. One comb of 390 cells, centre with very young larvae, outer cells with eggs, very few empty. Some cells with drops of honey, and the nest full of winged ants, 52 ♂ of *Paratrechina* (*Nylanderia*) *vividula* Nyl. (det. Donisthorpe); also one fragment of a Nematocerous fly.

Nest 236, Tukeit-Kaieieur trail, beneath leaf of small shrub, 4 ft. from ground, 10.ix. It consisted of a single comb of 141 cells, none used before, containing only eggs and young larvae. A few cells had some drops of honey.

Nest 203, edge of Kaieieur Savannah, beneath leaf of the Bromeliad, *Brocchinia micrantha* (Baker) Mer., 3 ft. from ground on stream bank, 5.ix. One comb of 185 cells, 9 cocoons near centre, surrounded by larvae, outer cells with eggs. A few cells with groups of honey. The queens in this nest had ovaries comparable with those of intermediates in nest 145 (below), but in the latter they were called intermediates because there was one queen with a large number of ovarian eggs. There was no such queen in nest 203.

Nest 156, Kaieieur Savannah, beneath leaf of *Brocchinia micrantha*, 2 ft. from ground, 2.ix. One comb of 355 cells, 49 cocoons in centre, surrounded by large larvae, then smaller larvae and eggs, then many empty cells. One worker was heavily parasitised with round Gregarines.

Nest 145, Potaro R., Amatuk, beneath leaf of SCYTAMINEAE sp.; 3 ft. from ground, 31.viii. One comb of 380 cells, in centre with 28 cocoons, surrounded by half-grown and then young larvae, then eggs, then many empty cells.

Nest 146, same data. One comb of 461 cells, with a centre area of 63 cocoons or recently vacated cells, a few half-grown larvae round the edge, no eggs noted.

Nest 201, edge of Kaieteur Savannah, on stream bank, beneath leaf of *Brocchinia micrantha*, 3 ft. from ground, 5.ix. One comb of 284 cells, central ones being used for a second time, just outside this area a few pupae; most cells with eggs and very young larvae.

Nest 169, Kaieteur, open Savannah, beneath leaf of *Brocchinia micrantha*, 2 ft. from ground, 3.ix. One comb of 347 cells, eggs, larvae and cocoons scattered throughout; some of the central cells used before. A few cells with drops of honey.

Nest 164, Tukeit-Kaieteur trail, beneath leaf of Aroid, 3 ft. from ground, 3.ix. One comb of 306 cells; eggs, larvae and cocoons irregularly distributed. Cells used before (pl. 3, figs. 19-21).

Nest 208, Kaieteur, open Savannah, beneath leaf of *Brocchinia micrantha*, 2 ft. from ground, 5.ix. One comb of 260 cells, eggs, larvae and cocoons distributed throughout. Drops of honey in some cells. A large number of winged ants, 203 ♂ *Paratrechina (Nylanderia) vividula* Nyl. (det. Donisthorpe), stored in the cells. Most cells used before.

Nest 170, Kaieteur Savannah, beside stream, beneath leaf of *Brocchinia micrantha*, 3 ft. from ground, 3.ix. One comb of 240 cells; eggs, larvae and cocoons distributed throughout. Most cells used before. On 5.ix., on another leaf of the same plant, about 15 wasps (presumably ones not captured on 3.ix.) had built a small stalked comb with a flat top. On 7.ix., this nest had 9 wasps but apparently no eggs. On 9.ix., this nest consisted of 40 cells with 10 eggs; the 13 wasps consisted of 2 queens and 11 workers.

Nest 165, Tukeit-Kaieteur trail, beneath leaf of an Aroid, 3 ft. from ground, 3.ix. One comb of 335 cells; cocoons mostly near the edge, but some in the middle; eggs and larvae (mostly young) distributed throughout.

Nest 210, Kaieteur, high forest on edge of R. Potaro, beneath leaf of Aroid, 3 ft. from ground, 5.ix. Nest of the normal flattened shape, but with a second half-comb extending only half-way across the bottom of the upper comb. The entrance at the edge of the lower comb, beneath the centre of the upper one. Upper comb of 257 cells, all used before; eggs, larvae and cocoons all distributed throughout. A few cells with drops of honey. Lower comb of 363 cells; eggs, larvae and cocoons distributed throughout.

Nest 202, edge of Kaieteur Savannah, by stream beneath leaf of *Brocchinia micrantha*, 3 ft. from ground, 5.ix. One comb of 345 cells, mostly, except perhaps the outer ones, used before; eggs, larvae and cocoons, distributed throughout. The data of these is summarised in Table 17.

Besides the new, small nest described under no. 170, another (no. 222) was found beneath a leaf of *Brocchinia*, 7.ix., near where one of the other nests had been removed on 2-3.ix. It consisted of a small stalked comb of 7 cells, with 9 wasps and no eggs. On 9.ix., this nest was taken; there were then 17 cells but no eggs. The 8 wasps were all workers, except one which may have been an intermediate, though its ovaries were only slightly developed, with no rudiments much larger than the others.

A nest, probably of this species (no. 228), was found on 7.ix., in high forest on the edge of the Kaieteur Savannah, beneath a drooping palm leaf, 3 ft. from the ground. On 8.ix. the nest was found to have been completely invaded by ants, *Wasmannia auropunctata* Rog. (det. Donisthorpe). It contained a few remains of dead wasp larvae but no adult wasps.

TABLE 17.

Nest data of *Polybia bistriata* (Fab.).

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	Eggs	♂	♂
166	390	70	0	6	10-13, 11-0	0		64	0
236	141	29	0	5	6-9, 7-4	0		24	0
203	185	27	1-2	16	1-3, 1-75	0		11	0
156	385	29	10-20	1	Many	2	none ripe	26	0
145	390	51	0	1	19	12	2-3	38	0
146	461	88	10-15	1	31	1	none ripe	86	0
201	284	37	1-2	3	7-9, 8-0	0		34	0
169	347	57	0	1	18	0		56	0
164	306	44	0	6	8-14, 11-2	0		38	0
208	260	49	0	1	17	0		48	0
170	240	99	15	27	2-5, 3-56	0		72	0
165	335	129	0	33	2-6, 4-0	0		96	0
210	620*	127	0	4	10-14, 12-0	0		108	15
202	345	93	1-2	5	11-20, 17-2	0		70	18

Nest no.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♂ + interm.	Eggs/ queens	Eggs/ ovarial eggs
166	0	145	200	45	0-37	5-6	2-3	33-3	3-0
236	0	70	71	0	0-40	4-9	2-5	14-2	1-9
203	9	56	120	0	0-62	6-9	5-1	7-5	4-3
156	49	136	100	108	0-65	13-3	4-9	100-0	
145	28	100	62	190	0-66	7-6	2-5	62-0	3-3
146	63	98	0	300	1-00	5-2	1-1	0	0
201	14	130	140	0	1-24	7-7	3-8	46-7	5-8
169	25	161	161	0	1-40	6-1	2-9	161-0	8-9
164	36	135	135	0	1-40	7-0	3-6	22-5	2-0
208	34	113	113	0	1-40	5-3	2-4	113-0	6-6
170	42	99	99	0	1-40	2-4	1-4	3-6	1-2
165	65	135	135	0	1-40	2-6	1-4	4-1	1-0
210	57	281	282	0	2-40	4-9	2-5	71-0	5-9
202	45	150	150	0	2-40	3-7	2-1	30-0	1-7

* Two combs of 257 and 363 cells.

All the wasps from these nests were preserved in alcohol, so the presence of sperm in the queens was not verified; they were identified from the condition of the ovaries. The line between queens and workers was nearly always sharp. The worker ovaries were filamentous with no developed rudiments. The queens nearly always had some ripe eggs and a number of enlarged rudiments, the number depending mainly on the number of queens in the nest (Table 18), but probably also on the stage of development of the nest, *i.e.* whether oviposition was at a maximum or not. Intermediates occurred in three nests, all of which had one queen. They differed from the workers

in having two or three rudiments more or less enlarged; they were quite different from the queens found in the same nests. The 16 queens in nest 203 would have been called intermediates if a typical queen had been found in that nest.

TABLE 18.

Effect of number of queens per nest on number of ovarian eggs in queens of *Polybia bistrata* (Fab.).

No. of queens per nest	No. of nests	Mean no. of ovarian eggs
1	5	21.0
3-6	6	11.3
16-33	3	3.4

The wing-lengths and numbers of hamuli in the female castes are also tabulated in Table 19.

TABLE 19.

Wing-lengths (mm.) and numbers of hamuli in ♀, intermediates and ♂ of *Polybia bistrata* (Fab.).

Caste	No. measured	Wing-length				Hamuli			
		6.0	6.5	7.0	Mean	5	6	7	Mean
♀	46	16	29	1	6.34	0	26	20	6.43
Interm.	14	3	11	0	6.39	1	7	6	6.36
♂	88	24	62	2	6.375	15	46	27	6.14

The difference in the mean number of hamuli between queens and workers is significant (P nearer to 0.01 than 0.02).

16. *Polybia bicyttarella* Rich. (p. 132).

This species entirely replaced *P. bistrata* (Fab.) and was common at Mazaruni Station, but both species were found on the Kaieteur Savannah, though the present one was not common there. A few specimens from Brazilian Guiana may, perhaps, also belong to the present species. The Guiana specimens differed consistently from *P. bistrata* in colour, but one series of that species from Amazonia showed little difference in this respect. Whenever a series from a nest is available, they appear easy to separate by the venation of the hind-wing.

Twelve nests of *P. bicyttarella* were found, but three of them were not fully investigated. The basic comb-number is two, but as the colony increases, a third, or even, in some cases, a fourth comb is constructed. The nest is an oblate spheroid, broadly attached to the underside of a leaf or twig, usually in relatively open situations. Two nests (nos. 162, 274) were more cylindrical. In the entrance is a circular hole at one side of the envelope below the lowest comb. The passage from the lower combs to the upper ones is always at one side of the comb, next to the envelope. The envelope and comb were

brownish-grey with some whitish streaks, the carton being of a crumbly texture and composed of small pieces of vegetable material, not fibrous. The cells are 2.9 mm. wide and 6.5-7.0 mm. deep. The width of 12 cells from four nests were measured with a micrometer, with the following results: min. 2.68, mean 2.85 ± 0.116 , max. 3.03 mm. The cocoons were attached to the rims of the cells and projected very strongly, by about 3.0 mm. Thus, compared with *P. bistriata* (p. 56), the cells are broader but shorter; as the wasp is a little larger (wing-length greater by about 0.5 mm.) the cocoons project a little more.

In Table 20, and in the account below, the nests are arranged in order of estimated age.

Nest 237, Tukeit-Kaieieur trail, small stalked nest beneath leaf of Aroid, 3 ft. from ground, 10.ix. One comb of 77 cells, the lower surface not yet covered by the envelope. The central cells had eggs, but the outer ones were empty.

Nest 41, Mazaruni Station, clearing, on *Citrus*, 4 ft. from ground, 17.viii. (pl. 3, fig. 24). The ant, *Dolichoderus* (*Hypoclinea*) *bidens* (L.) (det. Donisthorpe) was nesting on the same branch. There were two combs; the upper one was empty when examined but it is possible that ants had removed the eggs when the nest was on the table in the rest house. The lower comb was not covered by the envelope, and the cells were shallow, incomplete and empty. Comparison with other nests indicates that this nest was abnormal in the absence of brood. It may have been invaded by ants in the laboratory, as already suggested, or shortly before capture, or else the colony may have just constructed a new nest after some disturbance. The high average ovarian egg-number in the queens supports this view. Nine of the 49 workers captured had Gregarines in their guts; the same was true of two of the intermediates.

Nest 341, Mazaruni Station, clearing, attached with a rather broad base to twig of *Citrus*, 26.ix. The nest was ovoid, 5.0×1.2 cm. at bottom and about 3.7 cm. diameter at the top. There was a flange-like projection from the bottom of the envelope. There were two combs, the top one containing larvae from small to moderate size, the lower empty, except for drops of honey in about half the cells.

Nest 104, Mazaruni Station, second-growth forest, attached to liane about 5 ft. from ground, 24.viii. (pl. 3, fig. 22). There were two combs, the lower one containing a central area of 20 cocoons with large and then small larvae arranged round them; the upper comb had 6 cocoons and the other cells empty; it is just possible that their contents had been removed by ants while the nest was awaiting examination. The envelope had two large and one small process from the bottom. The intermediates had unusually well-developed ovaries (4-6, mean 4.2 eggs), but there were no sperm in their spermathecae, whereas there were sperm in that of the queen. It was noted that there was no difference in the size of spermatheca in the three types of female.

Nest 290, Mazaruni Station, clearing, beneath mango leaf, 12 ft. from ground, 21.ix. There were two combs, the upper one containing 110 cocoons but some larvae and eggs also, and a few drops of honey; the lower one had a central area of 110 cocoons, surrounded by larvae and eggs. Thirty-nine of the workers and one queen (7 eggs) contained Gregarine parasites in the gut.

Nest 15, Mazaruni Station, clearing, beneath leaf of shrub growing on date-palm, 13.viii. The nest was nearly spherical, 5 cm. in diameter, with the exit-hole at the bottom. There were two combs, the upper one having about 30 cells in the centre being used again and containing eggs, these surrounded by 30 cocoons, and these by larvae, mainly rather small. The lower comb contained an irregular group of 33 cocoons in the centre, surrounded by larvae, half of which were quite large, and some outer cells with eggs. The nest was full of winged ants, *Typhlomyrmex richardsi* Donisthorpe, 73 ♂ kept out of about 219 present. The 56 wasps were caught in tubes placed over the entrance, and 3 were lost. The order in which the wasps came out was not recorded, but most of the intermediates and the queen were found in one tube and probably came out last. The queen had much more developed ovaries than any intermediate and was the only one with sperm. The 9 intermediates had 1-6 eggs (mean 3.2). Most of the eggs looked unripe and possibly degenerate. They were smaller and transparent, whereas the normal ripe egg usually has at least patches which are white and opaque.

Nest 171, Kaieteur Savannah, beneath leaf of the Bromeliad, *Brocchinia micrantha* (Baker) Mer, 3.ix. There were two combs, the upper one containing cells which had been used before, with larvae and eggs irregularly distributed, and 10 cocoons dotted about; in the lower one the cells had not been used before and contained eggs and very young larvae, with drops of honey in some cells.

Nest 274, Mazaruni Station, clearing, beneath twig of mango, 8 ft. from ground, 18.ix. The nest was cylindrical, 50×2.5 cm. There were four combs; the top one with 41 cocoons, interspersed with larvae; the second, mainly larvae, with 26 cocoons round the edge; third, a central group of 10 cocoons, the rest mainly moderate-sized larvae; bottom comb, not enclosed by the envelope, cells very shallow and empty. Five of the workers and four of the queens contained Gregarines of various types in the gut.

Nest 283, Mazaruni Station, clearing, beneath leaf of mango, 12 ft. from ground, 19.ix. The nest was attached to the mid-rib of the leaf by an area 2.0×11.0 mm., and the bottom of the envelope was produced into a slight beak-like projection. The exit-hole was at the side, between combs 2 and 3. There were three combs, the top one with all the cells used before, containing mainly eggs but also 9 cocoons and a moderate number of large larvae dispersed at random. The second comb, with all cells used before, contained 26 cocoons and many larvae in the centre, eggs less numerous. The bottom comb, with all cells used before, contained 51 cocoons, many larvae and a few eggs. Both the condition of the combs and the presence of males show that this was a mature nest. The wasps were kept too long before dissection, and the ovaries were not well enough preserved to allow the eggs to be counted.

Nest 162 (pl. 3, fig. 23), Kaieteur Savannah, beneath downward-bent leaf of *Brocchinia micrantha*, 3.ix. The nest was irregularly cylindrical, 7.5×5.0 cm., with a short stalk 12.0 mm. in diameter. The entrance was on one side, beneath the bottom comb. There were three combs, the top one, with all cells used before, containing mostly eggs and larvae, but 37 cocoons in the centre; the second, also with all cells used before, had 90 cocoons in the centre, with eggs and larvae outside; in the bottom comb the cells had not

TABLE 20.
Nest data for *Polybia bicyttarella* sp. n.

Nest no.	Cells	Wasps	Wasps lost	♀	♂	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♀ + intern.	Eggs/ queens	Eggs/ ovalid eggs
237	77	33	0	1	10	9	1-3	23	0	0-10	23-0	0	30-0	3-0
41	143	55	30	4*	14-24, 13-3	2		49	0	[0-10]	5-9	0	35-8	2-1
	180													
	323													
341	136	108	0	10	3-8, 6-9	0		98	0	0-40	3-0	1-4	0	0
	190								0					
	326								190					
104	105	25	?	1*	24	5	4-2	19	0	0-67	9-7	4-9	?	?
	137		many						?					
	242								0					
290	184	105	6	23*	5-12, 6-5	0		82	0	0-79	4-4	1-5	5-2	0-8
	274								0					
	458								0					
15	110	56	0	1*	18	9	3-2	46	0	1-10	5-1	2-4	91-0	5-1
	174								0					
	174								0					
171	174	37	0	1	10	6	1-3	30	0	1-40	7-8	3-9	140-0	14-0
	116								0					
	290								0					
274	99	97	0	6	4-11, 7-7	0		91	0	1-40	3-6	2-4	0	0
	116								0					
	79								0					
	58								58					
	352								0					
283	129	143	0	4	?	0		116	23	2-49	3-4	2-1	41-0	?
	149								0					
	212								0					
	490								0					
162	157	84	0	6	9-17, 12-3	0		67	11	2-70	6-8	3-0	33-2	2-7
	168								0					
	243								0					
	568								43					

* Queens examined for sperm.

been used before and contained eggs and young larvae, with the cells near the entrance empty.

Nest 342, Mazaruni Station, clearing, beneath *Citrus* twig, 6 ft. from ground, 26.ix. The envelope included the bases of two leaves and had three flange-like projections beneath. 209 wasps were captured, and perhaps as many as 6 were lost. 100 were dissected, and included: 3 queens (with sperm, 16, 18, 20 eggs), 1 intermediate (1 developed egg), 69 workers (ovarioles filamentous), 27 males. The whole colony, therefore, may have contained 6 ♀, 2 intermediates, 145 ♂ and 56 ♂. The combs were not examined.

Nest 172, Kaieteur Savannah, beneath leaf of *Brocchinia micrantha*, 3.ix. The nest was lost before it was described. It contained 43 workers and 6 queens of the intermediate type (spermatheca not examined) with 1, 1, 1, 1, 2, 2 eggs.

It was noticed in this species, though not apparently in any of the others except perhaps *P. catillifex* Moebius, that there seems to be some relation between the number of queens in the nest and the number of cells in the first comb constructed, as shown below:—

Number of cells in comb 1		Number of nests	Number of queens	
Range	Mean		Range	Mean
77-110	98	4	1-6	2.25
129-143	136	3	4-10	6.00
158-184	172	3	1-23	10.00

There is no similar relation between the total number of wasps and the number of cells in comb 1.

The wing-lengths and hamuli-numbers were recorded in 20 queens (11 nests), 13 intermediates (6 nests) and 24 workers (12 nests), as shown in Table 21.

TABLE 21.

Wing-length and hamuli-number in *Polybia bicyttarella* sp. n.

Caste	No. measured	Hamuli					Wing-length (mm.)			
		5	6	7	8	Mean	6.0	6.5	7.5	Mean
♀	20	1	5	11	3	6.80	0	6	14	6.85
Interm.	13	0	3	9	1	6.85	1	8	4	6.62
♂	24	0	4	20	0	6.83	0	7	17	6.85

There is no sign of any differentiation; nor was there any difference in colour-pattern.

17. *Polybia procelloso* Zavattari var. *dubitata* Ducke, 1910.

This species was recorded by Bequaert (1944: 288) from BRITISH GUIANA: Kurupung, and is also known from the Amazon Basin and from Peru, while the typical variety occurs in Ecuador. In the British Museum collection are 2 ♀ BRITISH GUIANA: Canister Falls, xi.1919 (Cattle Trail Survey, A. A.

Abrahams). We caught two females—Mazaruni Station, second-growth forest, 29.viii.1937; Potaro R., Tukeit trail, 1.ix.1937. The nesting habits are unknown.

18. *Polybia catillifex* Moebius, 1856.

Bequaert (1944:288) records this species from BRITISH GUIANA: Turesi Falls; Kamakusa; Bartica; Pakaraima Mts. It is also known from Dutch Guiana, Brazil, Ecuador, Colombia and Peru. The British Museum collection includes a number of Brazilian specimens, including one determined by Ducke. The Oxford University Expedition obtained one specimen—Essequibo R., Moraballi Creek, dark forest, 24.ix.1929.

The nest was described and figured by Moebius (1856:16, pl. viii, fig. 4) and, as *Polybia septentrionalis*, by R. von Ihering (1904:269, pl. vi, fig. 10). It is small, of two or three combs, and the envelope is produced into several broad processes at the levels of its junction with the combs.

In 1937 four nests were found, all attached beneath creepers on large boulders on the edge of the Tukeit-Kaieteur trail. Each nest had one or two of the characteristic spout-like projections from the envelope. In two of the nests the envelope was dark brown, and in two with white streaks and blotches. It was thick and crumbly in texture, made of small elongate chips of vegetable material, not converted into fibres. The cells were 13.0×3.5 mm., and the cocoons were slightly domed, but mostly attached 0.5 mm. below the rim of the cell, so that they did not project. The nests described below are arranged in order of estimated age.

Nest 234, attached to both upper and under surfaces of the edge of Aroid leaf, 9.ix. The envelope had two short "spouts," and there was one comb of 91 cells, with a moderate-sized central area of young larvae and a larger outer one of eggs.

Nest 187, hanging from root, about 4 ft. from ground, 4.ix. There was one comb of 69 cells, containing eggs and larvae. One cell contained a drop of honey.

Nest 144, hanging from root beneath boulder, 4 ft. from ground, 1.i.x. There was one comb of 87 cells, completely surrounded by the envelope, and a second comb of 55 shallow cells, containing eggs, outside the envelope. The enclosed comb had an inner area of recently vacated cells containing eggs, and an outer ring of cocoons or full-grown larvae. As this nest contained males, it was presumably nearing the end of its cycle.

Nest 163, hanging from a root, about 6 cm. below boulder, 3 ft. from ground, 3.ix. There was a comb of 173 cells, surrounded by the envelope, and a second one of 66 cells outside the envelope. The inner comb had a central area of cocoons surrounded by larvae and eggs, the outer one had eggs in most of the cells.

Nest 244. A small comb of 11 cells, attached beneath a boulder, 2 ft. from ground, 10.ix. The cells were empty, and two wasps were present. It is likely that these were members of one of the other colonies which had been captured near this spot during the previous week.

The data of the first four nests are given in Table 21A.

TABLE 21A.

Data of four nests of *Polybia catillifex* Moebius.

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	♂	♂
234	91	17	0	4	1-3, 2-25	0	13	0
187	69	6	0	1	6	0	5	0
144	87 55	24	0	1	14	0	21	2
	142							
163	173 66	41	0	5	7-13, 9-4	0	36	0
	239							

Nest No.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♀	Eggs/ queens	Eggs/ ovarial eggs
234	0	31	60	0	0-34	5-4	2-4	15-0	6-7
187	0	33	36	0	0-40	11-5	6-6	36-0	6-0
144	27 0	33 0	27 55	0 0	1-10	6-5	1-6	82-0	5-9
	27	33	82	0					
163	74 0	60 0	39 50	0 16	1-77	5-8	1-7	17-8	1-9
	74	60	89	16					

It would appear from these Guiana nests that the cycle of this species is short, probably capable of completion in two combs. The initial colony was of 70-180 cells. It will be noted, in the above table, that the number of queens appears to be related directly to the number of cells in the first comb.

Five characters of 8 queens and 8 workers from 4 nests were measured with a screw-eyepiece micrometer, but none of them (width vertex, length mesonotum, length of abdominal tergite 1, (a) from dorsal muscle to point where sides diverge, (b) from this point to posterior margin, width of posterior margin) differed significantly.

Wing-length and hamuli-number were measured in 10 ♀ and 33 ♂. The means were ♀ 9.94 mm., 7.40; ♂ 10.00 mm., 7.70. These differences are not significant.

19. *Polybia singularis* Ducke, 1909.

This species was recorded by Bequaert (1944 : 288) from BRITISH GUIANA : Bartica district and Source of Essequibo R. It is also known from Colombia, Peru and the Amazons. In the British Museum collection there is a specimen from BRITISH GUIANA : confluence of Oronoque and New Rivers, 650 ft., ix.-xii.1937, 1 ♀.

The nesting habits were first elucidated by Ducke (1905b : 680, pl. 4, fig. 17, as *P. emaciata*). It is one of a small group of species which build their nests mainly of mud instead of vegetable carton. The nest is unique in having the

entrance in the form of a vertical slit down one side of the globular envelope. The slit corresponds to a nick in the edge of each comb. Earlier accounts of the nests without any knowledge of the wasps which made them were given by Smith (1851) and Lucas (1890). The nests seem always to be small, probably of not more than three combs.

20. *Polybia emaciata* Lucas, 1879.

Polybia fasciata of authors, not of Lepeletier, 1836.

Although known from Mexico (coll. B.M.) to Peru and Brazil, no specimens of this wasp seem actually to have been caught in British Guiana.

We found a mud nest, Mazaruni Station, second-growth, swampy palm forest, 17.viii.1937. It was attached beneath leaf, but had been completely invaded by the ant, *Neoponera unidentata* Mayr (det. Donisthorpe). Another nest of the same ant was found nearby in the bottom of an earthen termite nest, on a tree trunk, 3 ft. from the ground.

The nest has often been described and figured, the use of mud by a social wasp naturally attracting attention, though there is said to be some carton in the comb. Accounts will be found in Moebius (1856: pl. vi, fig. 1, as *Polybia cayennensis*), Lucas (1879), du Buysson (1899, as *Polybia phthisica*), Schulz (1904: 795), Rau (1933: figs. 23-28, as *Polybia fasciata*), and elsewhere. The nest is cylindrical or globular, of three or four combs, with a small circular exit-hole, and the intercommunications between the combs quite lateral.

21. *Polybia tinctipennis* Fox var. *nebulosa* Bequaert, 1943.

The typical form of this species is known from C. America, Peru and Brazil. The variety was described from BRITISH GUIANA: Kamakusa; Kartabo; Source of Essequibo R. It is also known from Trinidad. In the British Museum collection are the following specimens: BRITISH GUIANA: North-west district, Issororo, vii. 918, 2 ♀, 13 ♂ (C. B. Williams). TRINIDAD: 4 ♀ (E. B. Connell). The nest is not known.

22. *Polybia rufitarsis* Ducke, 1904.

Ducke (1910: 502) records this species from Amazonia and Brazilian Guiana, and Bequaert (1944: 289) from BRITISH GUIANA: Essequibo R., Moraballi Creek. In the British Museum collection are the following specimens:—BRAZIL: Obidos, 1904, ♀ (Ducke); Pará, 2 ♀; Lower Amazon, Parintins, 4.ii.1896, ♀ (E. E. Austen). BRITISH GUIANA: Essequibo R., Moraballi Creek, 5.ix.1929, 9 ♀ (Oxford Univ. Exped., specimens seen by Bequaert); New River, 700 ft., 23.i.1938, 4 ♀ (C. A. Hudson).

Ducke (*loc. cit.*) briefly states that the nest is of the normal ovoid type usual in this genus. The Moraballi nest, no. 1619, was found by one of our Indians, Jothan, attached on several spines on the stem of a spiny palm, 3 ft. from the ground, in high forest. The nest was ovoid, broadest at the bottom. The envelope was of very soft, red-brown carton, with an exit-hole, 18 mm. in diameter, on one side, near the bottom. There were four combs interconnected by a passage way adjacent to the envelope above the exit-hole. The cells were 12 mm. long, and the cocoons projected 5 mm. beyond their rims.

Top comb : 43 mm. diam. About 19 cocoons forming a ring round a central area of eggs and larvae. Outside this, more eggs.

Second comb : 62 mm. diam. Larvae in the centre, then a ring of cocoons, then a few eggs. Evidently, the first two combs were being used a second time.

Third comb : 62 mm. diam. Mainly cocoons.

Bottom comb : 75 mm. diam. ; 16 cells wide across the middle. Eggs in all the outer cells, but a considerable number in the centre empty.

73 ♀ wasps were captured, but probably rather more than 10 were lost.

23. *Polybia ignobilis* (Haliday, 1836).

P. atra de Saussure, 1854.

This species, which is known from Panama to Argentina, was recorded by Bequaert (1944 : 289) from BRITISH GUIANA : Mt. Roraima. In the British Museum collection are 2 ♀, BRITISH GUIANA : Rupununi district, 1919 (*Rev. F. Robinson*). The species must be uncommon in Guiana, but becomes abundant in S. Brazil, being an inhabitant of savannahs. According to Ducke (1910 : 503), the nest is nearly always built in holes in the ground ; he knew of only one exception, a nest built amongst the branches of a Cactus, and he suggests that records of nests in trees are due to misidentifications. Hase (1936), however, has given a long account of a nest which he found at Venezuela : Puerto la Cruz, beneath the roof of a verandah. The nest was an irregular ovoid 18.0 × 21.5 cm., and 12.5 cm. high. It had four completed combs and a fifth one under construction. It contained 1528 (unsexed) wasps, something over 1000 eggs, 233 larvae and 825 cocoons. A sample of 226 wasps examined later, included 87 ♂ : 139 ♀. As some of the combs were apparently being used a second time and males were present, the colony must have been fairly mature. Since a high proportion of eggs was also present, this suggests that *P. ignobilis* may be one of the species with long-living colonies which do not break up after swarming. According to Ducke, the comb may contain a considerable quantity of honey, especially at the beginning of the dry season.

The following insects have been recorded as closely resembling *Polybia ignobilis* (Hal.) in appearance : *Montezumia petiolata* Sauss., *Eumenes laevi-ventris* Fox, *Odynerus paraguayensis* Brèthes, VESPIDAE ; *Seminota marginata* Westw., TRIGONALIDAE ; *Cerioides barbipes* Loew, SYRPHIDAE ; *Pseudosphex noverca* Schaus, SYNTOMIDAE (Ducke, 1910 : 460 ; Bertoni, 1911 : 101, 121 ; Schrottky, 1915).

13. *Apoica* Lepeletier, 1836.

This is a very distinct genus of nocturnal wasps, and, like some other Hymenoptera with this habit, the ocelli are enlarged and the integument is more or less pale. It is also exceptional in the POLYBINAЕ in having the anal lobe of the hind-wing very reduced. In the works of du Buysson (1906), Ducke (1910) and Bequaert (1943a) it is held that the genus includes a single species which is found in several distinct colour-patterns. Schulz (1905 : 124) has, however, already pointed out that the inhabitants of any one nest all belong to the same colour-form, and further study has shown that the five varieties recognised by Bequaert are species which can be distinguished by structure as well as by colour. We understand that Dr. Bequaert has, independently, reached the same conclusion with regard to *A. arborea* Sauss.

The genus as a whole is known from southern Mexico and Grenada to Peru and Paraguay.

The nests are as distinctive as their inhabitants. They are gymnodomous and essentially sessile, the first four cells (du Buysson, 1906 : 338) being built on a little platform beneath a branch. In its final form the nest is a very flat cone, the base (formed by the open ends of the cells) being somewhat curved. Typically, the nests are about 20.0 cm. diameter, but they may reach 29.0 cm. diameter and 15 cm. thick (du Buysson, *loc. cit.*). They are built, not of carton, but of plant-hairs gummed together (Rau, 1933 : 143). Since the wasps are only active at night, the nests are a striking sight in the day-time, with the inhabitants densely packed all over the under surface of the comb. After dark, the wasps are often attracted to light; according to FitzGerald (1938 : 190), the wasps have been seen carrying caterpillars, and have also been caught covered with pollen. Ducke's (1905) description of a swarm consisting of 200 ♀-♀ and 5 ♂ flying by day sounds like the swarm produced by destroying a nest. It may have no bearing on the normal method of colony-founding, though this is only speculation. Figures of the nests have been published by de Saussure (1854 : pl. 28), Ducke (1904 : pl. 2, fig. 9), du Buysson (1906 : pl. 13), FitzGerald (1938 : pl. 3, fig. 11), etc. It is not yet possible to discuss differences between the nests of the species since the records rarely distinguish them. A preliminary taxonomic revision of the wasps will be found in Appendix 2 (p. 150).

1. *Apoica arborea* Saussure, 1854.

This species is not uncommon in British Guiana and also occurs on the Lower Amazon. It is much the most distinct of the species in the genus, but the nest, unfortunately, has not been described.

2. *Apoica thoracica* du Buysson, 1906.

This species is widespread in British Guiana, as also in S. America. A nest (no. 1999) was found hanging beneath a twig, 4 ft. above Moraballi Creek, Essequibo R., 12.ix.1929 (*Oxford Univ. Exped.*). The diameter of the comb was 12.5 cm., and the radius of the conical roof 7.5 cm. The supporting twig passed through the comb to one side of the centre. There were 25 cells in the central line, and about 490 in all, their diameter being about 5.0 mm. The colour of the comb was a yellowish-brown. The large central area of cells which contained cocoons was somewhat raised above the others, which contained next larvae, then eggs. The eggs were white, and 2.25 mm. long, and the cocoon-caps thin, whitish-transparent, not domed but a little below the level of the cell-rim. When the branch was cut, the nest fell into the stream, and the wasps flew about for some time and then settled on a leaf about 2 ft. above the old nest-site and formed a compact swarm, 7.5 × 2.5 cm. In this way 235 wasps were caught and one was lost. The sting was very painful.

3. *Apoica albomacula* (Fabricius [1805]).

This is the least known species in the genus and, since its description, has only been recognised by Bequaert (1944). It is only known from Dutch and British Guianas, where it seems to be rather local.

Nest 1368 (pl. 3, fig. 25), Essequibo R., Moraballi Creek, 2.ix.1929 (*Oxford Univ. Exped.*), was hanging beneath a branch, about 6 ft. above the ground, in a comparatively sunny place, near the creek. The wasps showed no activity by day, unless the nest was touched, when they swarmed on to the upper surface of the comb with their abdomens pointing outwards. All 58 wasps were caught; no queen could be recognised without dissection, and all the wasps were very uniform in colour. The comb consisted of about 200 cells, with about 70 cocoons, 20 larvae, 65 eggs and 50 empty. A group of 21 cells, at the centre, were being used for the second time.

4. *Apoica pallida* (Olivier, 1791).

This is one of the commonest and most widespread species, and probably a good many of the published accounts of the biology really refer to it. It is widespread in British Guiana. Berton (1911:181) bred the Trigonid, *Seminota marginata* Westw., as a parasite in Paraguay. FitzGerald (1938:105) records the colour-resemblance between it and the nocturnal Conopid fly, *Dalmannia* sp., in Trinidad.

5. *Apoica pallens* (Fabricius [1805]).

This is probably the commonest species of the genus, both in British Guiana and elsewhere. It is variable in colour and size but it has not so far been possible to recognise subspecies.

14. *Stelopolybia* Ducke, 1910.

This genus, as stated on p. 12, raises one of the most difficult problems in the taxonomy of the POLYBIINAE. The nests fall into two distinct types, the stelocyttarous gymnodomous type of most species, and the stelocyttarous calyptodomous type of *S. pallens* (Lep.) (= *infernalis* (Sauss.)) and two allied species. The first type, probably as a consequence of the absence of the envelope, is built in hollow trees or in other enclosed spaces; the second type is built hanging free from a leaf or twig. Ducke (1914) intended to found a new genus, *Gymnopolybia*, for the first group but, owing to an accident of type-fixation, *Gymnopolybia* Ducke, 1914 is a synonym of *Stelopolybia* Ducke, 1910. Araujo (1946) has recently proposed the genus *Angiopolybia* (type *Rhopalidia pallens* Lepeletier, 1836), so that valid names are available for both groups.

Although the two types of nest are very distinct, it is very difficult to find reliable generic characters by which to separate the wasps which build them. The characters given originally by Ducke (1910) are not satisfactory. Richards (1943) recorded a few more characters, but even in that work the genera are not well defined, partly because one species, *S. cajennensis* (Fab.), is to some extent intermediate. Araujo's paper (1946) did not bring forward any new structural characters. One additional small difference has recently been noticed—in *Angiopolybia* the propodeum tends to have a more or less horizontal area behind the postscutellum, whereas in *Stelopolybia* the propodeum falls immediately and almost vertically. It is proposed, in the present account, to treat *Angiopolybia* as a subgenus of *Stelopolybia*.

There is a further difficulty in connection with a number of Indo-Malayan

species usually placed in the genus *Parapolybia* Saussure, 1854. At the moment, no reliable character has been proposed to separate *Parapolybia* Sauss. from *Stelopolybia* Ducke. The nests seem to be similar, and if later study fails to differentiate them *Parapolybia* will have to be used as the earlier name.

With the present arrangement, *Angiopolybia* has three species found over most of the S. American rain forest, including British Guiana and Trinidad, but not C. America. *Stelopolybia* s.s. has about 12 species extending from Mexico to Paraguay. The most detailed information on a species of *Stelopolybia* concerns *S. vicina* (Sauss.), a very common species in southern Brazil. According to R. von Ihering (1903a; 1904), very large nests of several flat combs, joined by many pillars, are built in various sheltered situations. He gives information as to the number of queens in dissected samples.

The species of *Stelopolybia* are some of the most abundant and aggressive of South American wasps. They form a high proportion of the Polybiines encountered in casual collecting. A variety of other insects resemble them more or less closely in colour and appearance.

1. *Stelopolybia constructrix* (de Saussure, 1854).

This species was recorded by Bodkin (1917) from BRITISH GUIANA: Tumatumari, and by Bequaert (1944: 295) from Pakaraimo Mts.; Kamakusa; Kartabo; Source of Essequibo R. In the British Museum collection are the following specimens:—BRITISH GUIANA: Kutari Sources, 10.i.–10.ii.1936, ♀ (*G. A. Hudson*); Tumatumari, xii.1915, ♀ (*G. E. Bodkin*, Dept. Agric.); Cuyuni R., 3 miles above Kartabo, 20.ix.1937, 3 ♀ (*Richards and Smart*); Kartabo, vi.1932, ♀ (*M. D. Haviland*); Essequibo R., Moraballi Creek, 15.viii.–27.ix.1929, 4 ♀, Wallabah Bush, 7–12.xi.1929, 2 ♀ (*Oxford Univ. Exped.*). The species is also known from French Guiana and from Amazonia. It seems to be moderately common in high rain forest. The nest has not been described.

2. *Stelopolybia testacea* (Fabricius [1805]).

This species was recorded from British Guiana by Cameron (1912) as *Polybia flavicans*, and by Bequaert (1944: 296) from Kartabo; West bank of Demerara R.; Bartica; Pakaraimo Mts.; Kuyuwini R.; Oko R.; Mt. Roraima. It is also known from French and Dutch Guianas, Brazil, Venezuela, Bolivia and Peru. Besides Cameron's specimen, the British Museum has the following: BRITISH GUIANA: Kutari Sources, 10.ii–10.iii.1936, ♀ (*G. A. Hudson*); confluence of Oronoque and New Rivers, 650 ft., ix.–xii.1937, 2 ♀; New River, 750 ft., 16–17.iii.1938, ♀ (*G. A. Hudson*); Potaro R., ii.1908, ♀ (*S. M. Klages*); Tumatumari, xii.1915, ♀ (*G. E. Bodkin*, Dept. Agric.); Potaro George, near Tukeit, 9. ix. 1937, 4 ♀ (*Richards and Smart*); Mazaruni Station, high forest, 16.viii., 2 ♀, at sap, 21.viii.1937, 4 ♀ (*Richards and Smart*); Essequibo R., Moraballi Creek, Wallabah Bush, 12.xi.1929, ♀ (*Oxford Univ. Exped.*); North-west district, Issororo, vii.1916, ♀ (*C. B. Williams*). Like the previous species, the present one is common in high rain forest, but the nest is undescribed. Insects more or less closely resembling *S. testacea* in colour are: *Mischocyttarus flavicans* (Fab.), *Polistes testaceicolor* J. Beq. (*analys auct.*), *P. erythrogaster* Ducke var. *moraballi* Rich., *Montezumia analis* Sauss.,

Pachymenes orellana (Schulz) (VESPIDAE); *Rathymus cristatus* Ducke, *Odyneropsis vespiformis* Ducke (APIDAE); *Dasypogon intactus* Wied. (Dipt., ASILIDAE); SYNTOMIDAE sp. (Lepidopt.) (Ducke, 1910: 460; Study, 1926: pl. 14).

3. *Stelopolybia angulata* (Fabricius [1805]).

This species was recorded from British Guiana by Cameron (1912) under the name *Megacanthopus ruficornis* (type ♀ in coll. B.M.). Bequaert (1944: 296) records it from BRITISH GUIANA: Kaieteur; Bartica; Kamakusa; Arakaka; West bank of Demerara R.; North-west district, Warina; Pakaraimo Mts.; Mt. Roraima. It is also known from Venezuela, Dutch Guiana, Brazil, Ecuador, Peru and Bolivia. Specimens in the British Museum collection are from BRITISH GUIANA: Potaro R., Tukeit trail, 3-9.ix.1937, 12 ♀ (*Richards and Smart*); Mazaruni Station, clearing, 13.viii.-23.ix.1937, 5 ♀; second-growth forest, 14.viii.-24.ix.1937, 7 ♀; second-growth forest, on carrion, 27-28.viii. and 23-24.ix.1937, 32 ♀ (*Richards and Smart*); Essequibo R., Weri-Weri-kuru Creek, 15.x.1922, ♀ (*L. S. Hohenkirk*, Dept. Agric.); no precise locality, ♀ (*J. Rodway*).

Three females in the British Museum collection from Paraguay: Puerto Bertoni differ from the ordinary form of the species in having the pronotal keel less lobate at the sides, though more so than in *S. panamensis* (Cameron), the Central American species. The Paraguayan females also have the anterior tibiae entirely, or almost entirely, dark. In typical *S. angulata* they are markedly pale, at least antero-ventrally in all but 11 out of 65 ♀ specimens.

Two varieties of this species have been described with some yellow markings. One of these, var. *ornata* Ducke, 1905, is here recorded from British Guiana for the first time: Potaro R., Tukeit trail, high forest, 3.ix.1937, ♀ (*Richards and Smart*). Its pattern is as follows:—

Black; all tibiae and tarsi, distal and proximal ends of all femora, scutellar axillae and narrow anterior scutellar band, anterior half of post-scutellum, wide stripe on each side of propodeal furrow, bright yellow; mandibles dark; antennal flagellum reddish-orange.

Two other specimens in coll. B.M., ♀, Upper Amazon and ♀, S. Paulo, have rather more yellow than the above, particularly on the pronotum and, in the Amazonian specimen, two narrow stripes on the mesonotum. All three specimens agree in having the prominence in front of the pronotal fovea rather weaker than in typical *S. angulata*.

The other variety, var. *angulicollis* (Spinola, 1851), is not known from British Guiana, but the British Museum has two females from Pará. They have similar yellow markings on the legs but none on the thorax; the pronotal prefoveal prominence is also weak. These two varieties are more or less intermediate between *S. testacea* (Fab.) and *S. angulata* (Fab.) in both colour and structure.

S. angulata seems to be a characteristic species of low second-growth forest, where it is common and easily attracted to meat. It was not encountered at Moraballi Creek in an area of high forest, where the species abundantly attracted to carrion was *S. fulvo-fasciata* (Degerer). Ducke (1910: 520) has remarked that it is strange that nothing should be known of the nest of such a common species.

The distinctive appearance of *S. angulata* is closely approached by that of the following insects: *Polybia micans* Ducke var. *velutina* Ducke, *P. lugubris* Sauss., *Mischocyttarus carbonarius* (Sauss.), *Polistes melanostoma* Sauss., *P. deceptor* Schulz, *P. erythrogaster* Ducke var. *angulinus* Rich., *Pachymenes ater* Sauss., *Montezumia cortesia* Sauss. (VESPIDAE); *Odyneropsis foveata* Ducke (APIIDAE); *Polistomorpha sphegoides* Walk. (ICHTHEUMONIDAE); *Pseudosphex ichneumonea* H.-S. (Lep., SYNTOMIDAE), (Ducke, 1910: 460; Schulz, 1905: 119; Bertoni, 1911; Schrottky, 1915; and cf. Rothschild, 1931, for the *Pseudosphex*).

4. *Stelopolybia fulvo-fasciata* (Degeer, 1773).

Polybia vulgaris Ducke, 1904.

This species is common in British Guiana and is recorded by Bequaert (1944: 296) from many localities; there are more than 50 female specimens from British Guiana in the British Museum collection. It was found in clearings, in low second-growth forest and in high forest, but most commonly in the second habitat. It is much attracted to carrion and, according to Ducke (1910: 523), to fish drying in the sun, on the Amazons. Outside the Guianas, it is found from Colombia to Peru and Brazil, *i.e.* in the rain forest area. Ducke (*loc. cit.*) describes also a var. *mexicana*, from Mexico, but it seems possible that there was some error of labelling or of identification. The nests are built in hollow trees and one (no. 338) was found at Mazaruni Station, high forest in fallen tree (pl. 3, fig. 26), 25.ix.1937, by an Arawak attached to the Forestry Dept. The wasps were very aggressive, and no really satisfactory way of taking the nest could be devised. Finally, CS₂ was poured in and the entrance was stopped up. A very large number of wasps was now flying actively outside and stinging viciously; 891 were caught. On 26.ix. the nest was visited at 7.30 a.m., but there were still many wasps outside and 54 were caught. The nest was again dosed, and the entrance stopped up again. On 27.ix. there was still a number of active wasps outside, but on 28.ix. only a small number was present and 104 were caught. The tree was then sawn open, and the nest in a half-section of the hollow trunk was taken to the rest house: 360 dead wasps were found in the nest, as well as the 1049 captured outside. Of the former, 300 were dissected and 13 (4.6 per cent.) were queens; of the latter, 400 were dissected and all were workers. This suggests that the queens do not leave the nest like the workers, though the castes are not distinguishable externally. None of the dissected wasps seemed to be intermediates, though those taken from the nest were in bad condition for dissection. As this nest was taken on the last day of our visit, it could not be described at the time, and the larvae were decaying. During the war the nest was badly damaged so that only an incomplete account of it is possible. The combs started 22.5 cm. from the entrance, the comb nearest to which was the smallest and probably the last one made. The internal diameter of the hollow tree was about 20.0 cm., the wood being 1.5–5.0 cm. thick. There were 12–13 combs, of which 3–4 were small and the remainder extended more or less across the hollow. The combs were curved, so as to be convex in the centre, and attached by numerous pillars at their edges to the tree. The pillars were about 1.0 cm. long (or rather less) and 1.0–2.0 mm. diameter. The combs were set obliquely to the trunk, so that the cells almost

faced upwards. The bottoms of the cells were very little convex, and the under surface of the combs was hardly mamillated. The combs were composed of red-brown carton, dull, of very distinctly fibrous, felted material, looking almost like plant-hairs. Occasionally there were spots or bands of a lighter colour, and apparently some "windows" were left in the walls. The cells were 4.3 mm. in diameter, and the largest were 11.0 mm. long, but most of them were 3.0-5.0 long. As there were no cocoons, it seems likely that the whole nest was young. A very rough estimate of the number of cells was 25,800.

A comparison of 7 queens (the others were very imperfect) and 12 workers failed to show any real external difference. The lengths of the fore-wing and the numbers of hamuli were: queens, 11.5-13.0, mean 12.5 mm., 10-12, mean 11.0; workers, 12.0-14.0, mean 12.9 mm., 10-14, mean 11.6, but these differences are not statistically significant.

S. fulvo-fasciata (De G.) has a pattern which is more or less closely followed by a large number of other insects. We, ourselves, noticed the following: Homoptera—TETTIGELLINAE: *Lissocarta vespiformis* (Fab.) (det. Dr. J. W. Evans), ♀, Mazaruni Station, high forest, 16.ix., ♀, Kaieteur-Tukeit trail, high forest, 9.ix. The colour resemblance is rather striking in the live insect, but the Jassid is much smaller.

Heteroptera—MIRIDAE. Undescribed genus (det. Dr. W. E. China), 2 ♀, in high forest on edge of Kaieteur Savannah, 7.ix. The resemblance to a brown and yellow Polybiine is generalised and the bug is rather small.

Diptera—ASILIDAE. *Deromyia fasciata* Macq. (det. H. Oldroyd), Potaro R., Kaieteur Savannah, ♂, 5.ix., ♀, 10.ix., Tukeit trail, ♀, 3.ix. The size is about right, but the colour resemblance is generalised.

Diptera—STRATIOMYIDAE. *Chrysochlora longiseta* Walk., Mazaruni Station, second-growth forest, ♂, 21.viii., ♂, 26.viii. The colour resemblance is rather rough. The flies seem to have some association with the mounds of the leaf-cutting ant, *Atta*.

Neuroptera—MANTISPIDAE. *Climaciella* sp. (det. D. E. Kimmins), Mazaruni Station, second-growth forest, ♂, 14.viii., ♂, 25.viii. The second specimen was seen on a leaf and mistaken for some fly mimicking the Polybiine; then, when it moved its front legs, it was mistaken for a Polybiine eating a black fly. Finally, it hopped on to another leaf and it was recognised for a Mantispid. The colour resemblance is close, even in the dead insect, and is interesting because some members of the family are parasites of Polybiine wasp colonies. The following colour resemblances have been noted in the literature: *Mischocyttarus surinamensis* (Sauss.) and allies, *Pseudopolybia difficilis* (Ducke), *Pachymenes testaceus* Fox (VESPIDAE); *Osiris* sp. (APIDAE); *Polistomorpha fasciata* Westw. (ICHNEUMONIDAE); *Dasypogon* (*Diognites*) *intactus* Wied. (Dipt., ASILIDAE); Syntomid sp. (Lep.) (Ducke, 1910: 460; Study, 1926, pl. 14).

Rothschild (1931) records that the Syntomids *Sphecosoma trinitatis* Rothschild and *S. deceptrix* Hmps. resemble "*Polybia fasciata*"; this may be the present species or *Polybia emaciata* Lucas.

5. *Stelopolybia pallipes* (Olivier, 1791).

This is another common wasp, ranging from Mexico to Paraguay, but occurring in several colour-forms, more than one of which may be found in one

locality. The nest-populations required to decide the status of the varieties are not yet available. The wasps range widely, from clearings to dark forest, the carnivorous propensities of the whole genus probably accounting for their relative indifference to the type of vegetation.

Var. pallipes (Olivier, 1791).

Bequaert (1944:298) records this form from BRITISH GUIANA: Mt. Roraima and also from Brazil, Paraguay and Peru. There is one Guiana female in the British Museum collection: Upper Courentyne R., ix.1935, (*G. A. Hudson*).

Var. myrmecophila (Ducke, 1905).

Bequaert (1944:298) records this variety from BRITISH GUIANA: Source of Essequibo R.; Demerara R.; Rupununi R., and from GUATEMALA to PERU and BRAZIL.

British Museum specimens are from MEXICO (Guerrero, Tabasco), GUATEMALA, BRIT. HONDURAS (Belize, ♀, probably type of *Polybia pallipes* var. *centralis* Cameron, 1907), REPUBLIC of HONDURAS, NICARAGUA, COSTA RICA, PANAMA, BRAZIL (Céara, Bahia, Rio de Janeiro), ECUADOR and BRITISH GUIANA: Potaro R., Kaieteur Savannah, 9.ix.1937, ♀¹⁵ (*Richards and Smart*); Essequibo R., Moraballi Creek, Wallaba forest, 20.ix.1929, ♀, high forest, 18.x.1929, ♀ (*Oxford Univ. Exped.*).

This form of *S. pallipes* seems to be commonest in C. America and is rather rare in British Guiana.

Var. anceps (Saussure, 1854).

This variety has been misidentified by Bequaert (1944) and does not really occur in British Guiana. The type ♀, in the collection of the British Museum, is labelled "Brazil," and there is one other similar specimen, without any data. The description of these specimens is as follows:—

Female. Black; most of mandibles, ventral margin of clypeus, inner orbits from clypeus to top of ocular sinus, lower two-thirds of outer orbits, mouth-parts, keel and narrow posterior margin and spinacular tubercle of pronotum, pro-episternum, small spots on sides of scutellum and its axillae, narrow central band of postscutellum, moderately large spot at anterior dorsal corner of mesopleuron, minute spot on each side of tergite 1, very narrow posterior band of tergites 2-6, *lemon-yellow*. Antennal flagellum reddish-brown beneath, legs testaceous to brownish, coxae, 4 hind femora and hind tibiae darker. Tegulae brown. Wings hyaline, costal margin and radial cell narrowly brownish, venation brown. Length of fore-wing 9.5 mm.

Var. bequaerti var. n.

Stelopolybia pallipes var. *anceps* of Bequaert, 1944, not of Saussure.

This is the commonest form of the species in British Guiana, and was recorded by Bequaert (1944:298) from: Kamakusa; Kartabo; West bank of Demerara R., and also from Trinidad, Dutch Guiana, Venezuela, Colombia,

¹⁵ This specimen, which has unusually angulated sides to the first abdominal tergite, was misidentified by Richards (1943:48) as *Gymnopolybia sulfureofasciata* (Ducke).

Panama, Bolivia and Brazil. The dark markings are much less extensive than in the true var. *anceps*, described above.

Female. Head yellow; a U-shaped black mark above antennae, large occipital black band connected to U-shaped mark and to posterior corners of eyes. Antennae black, segments 1-2 yellow beneath, last 3-4 segments orange to brown beneath. Thorax yellow, spot in front of pronotal keel, oblique humeral marks, three stripes on mesonotum, central suffusion of scutellum, posterior margin of postscutellum, central line and short lateral lines and posterior margin of propodeum, black. Legs yellow. Tegula yellow with large central testaceous spot. Basicosta nearly all yellow. Wings hyaline, a little yellow-brown towards costa; length about 11.0 mm. Abdomen brownish-black, ventrally almost entirely yellow, dorsally with very narrow posterior margin to tergite 1, narrow base to tergite 2, narrow posterior bands to tergites 2-5, broad sides to tergite 6, yellow.

Male. Clypeus with ventral margin less angular, but as a whole longer, a little longer than broad, surface with silvery tomentum; eyes considerably larger, especially below, tempora narrower; antennae with 13 segments, those of flagellum all longer; 7th sternite broad and flat. Markings as in female, except: occipital black mark smaller, not connected to eyes; antennae orange-brown beneath; pronotum with two small black spots in front of keel and no humeral marks; scutellum with only narrow central line black, postscutellum yellow. Length of fore-wing 11.5 mm. Abdominal tergites 6-7 dark with narrow posterior yellow bands.

Type ♀, BRITISH GUIANA: Mazaruni Station, second-growth forest, 15.viii.1937 (*Richards and Smart*). Paratypes, BRITISH GUIANA: Mazaruni Station, in colony house, 11-28.viii., 4 ♀; clearing, 11-28.viii., 1 ♂, 5 ♀; second growth, 12.viii.-16.ix., 22 ♀ (8 on carrion); Cuyuni R., 3 m. above Kartabo, high forest, 20.ix., 2 ♀; Bartica-Potaro Rd., 70 miles point, nest in trees, 30.viii., 2 ♀; Potaro R., Kaieteur-Tukeit trail, 4.ix., 3 ♀; Kaieteur Savannah, 10.ix.1937, 1 ♀ (*Richards and Smart*); Essequibo R., Moraballi Creek, dark forest, 14-19.viii., 2 ♀; Wallaba forest, 19.x.-7.xi.1929, 2 ♀ (*Oxford Univ. Exped.*); Cuyuni R., Kamaria Landing, trail, 21.xi.1929, ♀ (*Oxford Univ. Exped.*); Cattle Trail Survey, Canister Falls, xi.1919, 3 ♀ (1 Dept. Agric.) (*A. A. Abrahams*); North-west district, Issororo, vi.-vii.1916, 4 ♀ (*G. E. Bodkin and C. B. Williams*). B.W.I., TRINIDAD: Mt. Tucuchi, 2-3000 ft., 17.i.1924, 3 ♀ (*S. A. Neave*); no precise locality, 6 ♀ (*E. B. Connell*) (variety with the yellow unusual bright and pale). VENEZUELA: Caracas Valley, "Las Ruices," 21.v.1926, ♀ (*H. E. Box*); Las Adjuntas, 959 m., 28.vi. and 4.vii.1926, 2 ♀ (*H. E. Box*); 5 m. S. of Caracas, El Valle, 3200 ft., 23.iii.1907, ♀ (*G. B. Longstaff*). BRAZIL: 1 ♀.

The single male specimen (clearing, 28.viii.) had a female Stresipteran beneath the centre of tergite 5; the host was unmodified. A further female was found on a mango leaf (Mazaruni Station, clearing, 22.viii.1937) which was dead with an entomogenous fungus, *Hirsutella saussurei* (Cooke) Speare (det. T. Petch).

The nest referred to above (Bartica-Potaro Road), was in a standing hollow tree, about 10.0 cm. diameter. There was a slit-like entrance, a natural fissure, guarded by a number of wasps. There was no time to stop and investigate it.

Ducke (1907: 182, pl. 1, fig. 1) has figured a nest of the var. *myrmecophila* which was found in an earthen termite nest, more or less attached to a nest of *Synoecca virginea* (Fab.) [*irina* (Spin.)], but few details can be made out in the figure. Bertoni (1911: 123), in Paraguay (varieties not stated), found it

nesting in holes in trees, in rocks, in deserted ants' nests, or any partly covered cavity; commonly in tree roots or in old nests of leaf-cutting ants, *Atta*. The combs were often very irregular, depending on the nature of the site. He found it abundant in forests, very carnivorous and with a painful sting. Strand (1912: 317, fig. 0) describes two nests found in Paraguay by Professor J. D. Anisits. One in a hollow tree, the other (figured) in the root of *Cedrella fissidens*. The wasps were very aggressive and continually came to the kitchen of his house to lick raw meat. The colony was destroyed with CS₂, and found to contain 500 wasps and 9 combs. Rau (1933: 88) made a number of observations on one of the varieties of the species in Panama: Barro Colorado Is., finding nests in a variety of protected situations, but always with the combs vertical. A colony found in the bamboo roof of a hut consisted of 75 wasps and one comb of 50 shallow, empty cells, so it must have been recently founded by a swarm. A much larger nest was found between a tree and a rock leaning against it. There were seven combs, the three largest about 20.0 × 8.7 cm. They contained 12,610 early stages, nearly all pupae, and there were 1965 adults. Apparently this colony was about to swarm, but it is not stated whether any males were present. FitzGerald (1938: 187, pl. 2, fig. 5) describes and figures a nest from Trinidad, where the species (probably var. *bequaertii*) is common in various types of forest. He describes a nest of 11 combs in which many cells were being used over again. He suggests that even such nests are not occupied for very long, and that the site is always deserted after a few weeks. It is not easy to reconcile this suggestion with the likely duration of the development of the early stages, unless by some coincidence all the nests he found happened to be mature. Myers (1937: 71), in Venezuela: Ocumare de la Costa, found the species taking honey-dew from a group of Homoptera, *Membracis* sp.

As might be expected from its wide-ranging and aggressive habits, this species is resembled in colour by a number of other insects. The following have been recorded: *Mischocyttarus surinamensis* (Sauss.), *Eumenes flavescens* Brèthes, *Eumenes* sp. (VESPIDAE); *Gorytes* sp. (SPHECOIDEA); *Poecilopompilus polistoides* (Smith), *P. mundiiformis* Rohw. (when flying) (POMPILIDAE); *Polistomorpha* sp. (ICHNEUMONIDAE); *Odontocera fasciata* Oliv. (when alive) (CERAMBYCIDAE); TIPULIDAE sp. (when flying, not when ovipositing) (DIPT.); SYNTOMIDAE sp. in Trinidad, *Pseudosphex metamelas* Hamps. (FitzGerald, 1939: 104; Bertoni, 1911: 124; Schrottky, 1915). Schrottky notes that the moth has colour-varieties corresponding to those of the wasp, but that it is very rare. Bertoni saw tanagers feeding on winged termites and noted that they retreated when one of the wasps approached, so that the resemblance may be of some advantage to the moth.

6. *Stelopolybia cajennensis* (Fabricius, 1798).

A common species, chiefly in open places in BRITISH GUIANA and recorded by Bequaert (1944: 294) from: Bartica; Kamakusa; N.W. district, Warina; Kartabo; Mazaruni Settlement; also from Rep. Honduras and Trinidad to Brazil and Peru. The British Museum collection has 33 ♀ from British Guiana, including 8 ♀ from nest 5886—Essequibo R., in hollow bamboo, 1.xi.1929 (*Oxford Univ. Exped.*). This nest was described as follows, by Mr. J. E. Duffield: "The nest was in a semi-horizontal bamboo, one end of which

formed the entrance. There was a single oval comb, about 3.7×11.2 cm., suspended from the roof. The comb was almost 12 mm. deep, but the cells were only 3–4 mm. long. The carton was light buff in colour. About 300 wasps were present." This must have been a very young colony, recently founded by a swarm. According to Ducke (1910:524) this species is well known to nest in hollow branches of trees; there do not, however, appear to be any detailed descriptions.

7. *Stelopolybia (Angiopolybia) pallens* (Lepeletier, 1836).

Polybia infernalis de Saussure, 1854.

Polybia ampullaria Moebius, 1856.

This is another species which is common in British Guiana, in high or second-growth forest, more rarely in open places. Bequaert (1944:294) records it from many British Guiana localities, and in the British Museum collection there are 8 ♂, 127 ♀ from this country, as well as material from several nests. Outside Guiana, it is known from Panama (Bugaba, ♀ (*Champion*)) and Trinidad to Brazil, Bolivia and Peru. The wasps vary somewhat in colour but perhaps hardly enough for the forms to be given names. In the common Guiana form the dorsum of abdomen is obscurely darker, especially posteriorly, with narrow pale bands at ends of tergites 1–3. In a very rare Brazilian type the abdomen is uniformly pale testaceous. The specimens from Trinidad have the abdomen unusually dark (also ventrally), with narrow, pale bands at the ends of tergites 2–3, and the ventral part of the thorax unusually bright yellow. A long series from a nest (New River, i.–ii.1938, 7 ♂, 38 ♀ (*C. A. Hudson*)) have the disc of the vertex, part of the sides of pro- and mesonotum, the end of tergite 2 and tergites 3–6 almost black. Associated with this material is *Brachymeria* sp., ♀ (CHALCIDIDAE), probably bred from the nest.

The nest (pl. 3, fig. 27; pl. 4, figs. 28–9) is a well-known object, a pear-shaped carton with a spout-like entrance at the bottom, hanging from a leaf or twig. Inside is a number of combs, hanging one beneath the other by fine pillars, but free from the envelope, except sometimes for a few pillars. It has been described and figured by Moebius (1856:13, pl. 7, fig. 1), Ducke (1910:524, fig. 12) and Williams (1928:154, pl. 27). Reid (1942:316, figs. 104–8) has described the larva.

On the Oxford University Expedition to British Guiana, 1929, three nests were obtained, and short notes on them are available.

Nest 2000, Essequibo R., Moraballi Creek, on small tree on edge of trail, 2 ft. from ground, 12.ix.1929. It was attached to three leaflets by a base almost as wide as the greatest diameter of the nest. The envelope was 7.5×10.0 at its widest and 10.0 cm. long, and the entrance-hole at the bottom was 2.5×1.2 cm. The envelope and combs were pale brown with darker brown streaks. The top comb was 4.3×2.8 cm., and was attached to the envelope by five narrow columns; it contained almost nothing but cocoons. The second comb was 5.0×3.5 cm., and was attached to the top one by three narrow columns and to the envelope by four narrow and one broad one; there was a circle of cocoons in the centre, surrounded by a ring of larvae, then eggs. The third comb was 4.3×3.0 cm., and was attached to the second one by two narrow columns; the cells were mostly empty but there were some larvae in the centre, surrounded by eggs. The cocoons projected about 1.0

mm. beyond the cells: 94 wasps were caught and very few were lost. The colony was evidently rather young and was still inhabited by the founder population only.

Nest 2001, Essequibo R., Moraballi Creek, on small tree, 1 ft. 6 in. from ground in Mora (*Dimorphandra*) forest, 12.ix.1929. It was attached to a small branch and a leaf at several points, and was considerably damaged in removal. The envelope was pale whitish-grey with darker streaks, about 7.5×3.7 cm. at the widest point. There were 3 or 4 combs, the largest, 3.3×2.5 cm.: 59 wasps were captured but many were lost.

Nest 4607, Essequibo R., 1 m. north of Monkey Jump, 21.x.1929. This was attached beneath a laurel-like leaf and contained three combs of 160, 160 and 100 cells. There were 90 wasps, probably the founding-population.

In 1937, five nests of this species were studied, but either none was very mature or, as is perhaps more likely, the type of cycle in this genus is different from that in the commoner species of *Polybia*. The thin, one-layered envelope was brown with grey streaks or (nest 288) pale stone-colour with brown streaks, fibrous, of a pliable texture. The cells were 7.0 mm. deep and 2.75 mm. broad, and the cocoon-caps were flush with the rims of the cells and little domed.

The queens in this species are little differentiated and in most of them the ovaries are in a condition which in *Polybia* would be called "intermediate." There was little relation between the presence of sperm and the degree of development of the ovaries. There were two very imperfectly separated categories of queens and intermediates, and workers, in which the ovaries were quite filamentous.

Nest 287, Mazaruni R., Kamaria Landing, beneath leaf of small tree, 2 ft. from ground, 20.ix. There were two combs, most of whose cells contained eggs, but some of them were still empty. All the wasps, to the number of 160, were captured and 100 were dissected, though their condition had deteriorated so that the numbers of eggs could not be counted. There were 3 queens with well-developed ovaries, 22 intermediates (some of which may have been queens), and 75 workers.

Nest 106 (pl. 3, fig. 27), Mazaruni Station, second-growth forest, beneath leaf of palm, 8 ft. from ground, 25.viii. This was an abnormal nest with two spout-like entrance tubes at the bottom. It is possible that the wasps were enlarging this nest and were in the middle of reconstructing the envelope. There was one large upper comb with a central area of cocoons, surrounded by larvae, eggs and empty cells; a small lower comb had half the cells empty. There were 85 wasps (probably very few were lost), and these consisted of 10 queens, 12 intermediates and 63 workers. The queens and intermediates both had small ovaries containing 1-4 egg-rudiments larger than the others, though not looking ripe; they differed only in that sperm were found in the spermathecae of the queens. No specimen looked like an ordinary *Polybia* queen.

Nest 255, Potaro gorge, beneath upright leaf of an Aroid, 2 ft. from ground, 11.ix. There were two combs and in the upper one a considerable area consisted of cells containing larvae and eggs, in cells being used a second time. The lower comb contained only eggs and young larvae. There were 25 wasps; 11 queens (3-7 eggs), 4 intermediates (2-3 larger but unripe rudiments), and 10 workers.

Nest 288, Mazaruni Station, second-growth forest, beneath leaf of palm,

7 ft. from ground, 21.ix. According to Mr. T. A. W. Davis, this nest had been present since July, but we doubted if we could have overlooked it for so long, being on the edge of one of the main trails. If, however, the cycle of this species is a long one, it is not unlikely that Mr. Davis was right. There were two combs, in both of which the different stages were irregularly distributed, indicating a nest of some age. 175 wasps were caught (about 4 being lost) and 100 were dissected: 58 were workers and 42 had more or less developed ovaries (2-4 enlarged egg-rudiments). Queens (32) only differed from the intermediates (10) in the presence of sperm. Those in which no sperm were found had the ovaries no less developed than those with sperm, and sperm were found in some with the least developed ovaries.

TABLE 22.

Data for five nests of *Stelopolybia pallens* (Lep.).

Nest no.	Cells	Wasps	Wasps lost	♀	Eggs	Interm.	♂	♂
287	164 99	160	0	4	?	35	121	0
	263							
106	260 26	85	0	10	2-5, 3-0	12	63	0
	286							
255	161 28	25	0	11	3-7, 5-3	4	10	0
	189							
288	275 140	175	4	56	2-4, 3-0	18	101	0
	415							
223	330 477 303 30	390	0	90	1-4, 2-5	47	253	0
	1140							

Nest no.	Cocoons	Larvae	Eggs	Empty	Age	Cells/ wasps	Larvae/ ♀ + interm.	Eggs/ queens	Eggs/ ovarial eggs
287	0 0	0 0	150 80	14 19	0-10	1-6	0	57-5	?
	0	0	230	33					
106	44 0	100 0	80 13	36 13	0-68	3-4	1-3	9-3	3-1
	44	100	93	49					
255	51 0	55 14	55 14	0 0	0-73	7-6	4-9	6-3	1-2
	51	69	69	0					
288	28 2	124 0	123 100	0 38	1-40	2-4	1-0	4-0	1-3
	30	124	223	38					
223	51 129 113 0	229 148 90 0	50 200 100 30	0 0 0 0	2-40	2-9	1-56	4-2	1-7
	293	467	380	0					

Nest 223 (pl. 3, fig. 26), Kaieteur Savannah, high forest by river, hanging from liane over the trail, 2 ft. from ground, 7.ix. The nest was about 17.5 cm. long, and two living leaves were incorporated to form part of the roof. There were four combs, the cells of the upper two being used for the second or probably the third time. All the wasps (390) were captured and 100 were dissected. There were 65 workers, 23 queens and 12 intermediates. The last two classes were barely distinguishable on the structure of the ovaries, and it was not possible to examine them for sperm. This is clearly a much older nest than the others and it is surprising that no males were present. In Table 22 the data of these nests are presented in more detail, arranged in estimated order of age.

No difference in external characters has been detected between workers, intermediates and queens.

Mean hamuli numbers for 27 queens, 16 intermediates and 30 workers were : 7.96, 8.19, 7.97, respectively. Larger numbers were measured for wing-length only, *viz.* 83 queens, 85 workers and 20 intermediates ; the averages were 8.13, 8.14 and 8.28 mm., respectively. The slightly higher averages for the intermediates were probably characteristic of the particular nests they were taken from, there being considerable variation from nest to nest. In 12 ♀, 12 intermediates and 12 workers from 5 nests, 5 characters (minimum width of vertex, length of mesonotum, length of first abdominal tergite from dorsal muscle to point where sides diverge, length from this point to posterior margin, width at posterior margin) were measured with a screw-eyepiece micrometer. All the corresponding means were exceedingly similar, and none differed significantly.

There is some suggestion in this species that the number of cells in the first comb may be related to the number of queens in the founding population, as shown below :—

No. of cells in comb 1	No. of queens	Cells per queen	Total no. of wasps
161	11	14.6	25
164	4	41.0	160
260	10	26.0	85
275	56	4.9	175
330	90	3.7	390

It may be noted that in this species the number of queens appears to increase regularly with the age of the colony. The data are, unfortunately, scanty ; they would be consistent with the reception into the nest of fertilised females at various times after foundation, but the phenomenon may be fortuitous.

8. *Stelopolybia* (*Angiopolybia*) *paraensis* (Spinola, 1851).

Bequaert (1944 : 294) records both the typical form and the var. *obscurior* Bequaert from British Guiana, but we have seen no specimens from that country. The species occurs in most of the South American rain forest from Panama to Amazonia and Ecuador. According to Schulz (1904 : 795) (quoted by Ducke, 1910 : 526), the nest is like that of *S. pallens*, but larger and without the tube-like production of the envelope at the exit-hole.

9. *Stelopolybia (Angiopolybia) obidensis* (Ducke, 1904).

This species is a characteristic inhabitant of the rain forests of Guiana and Amazonia, but is not known elsewhere. Bequaert (1944 : 295) records it from many localities in British Guiana, and in the British Museum collection are 44 females from Essequibo R., Moraballi Creek; Mazaruni Station, second-growth and high forest; Potaro R., Tukeit trail (medium forest) and Kaieteur Savannah. Bodkin (1917) records it from the R. Puruni, and there is a female from the Ituni Savannah (coll. Dept. Agric.). The wasps are often attracted to carrion, but the nests are unknown.

15. *Parachartergus* R. von Ihering, 1904.

There are at least eight well-marked species in this genus and some of them should probably be further divided. Four are known from British Guiana.

The nests are somewhat variable in structure, though all are stelocytтарous and calyptodomous. In some species each comb is separately supported by a pillar at one edge from a branch or a leaf, each comb being at right angles to the long axis of the nest. In others, several combs, each with its own pillar, hang beneath a leaf, the lower surface of which is covered by the envelope. In nests of this type the separate combs may eventually fuse to form a single larger one supported by several pillars. The exit-hole is at one end of the leaf-shaped envelope.

This and the next two genera provide another example in which the classification, based on the structure of the adult wasps, does not agree very well with one founded on nest architecture. Certain species from each genus make almost identical nests, whereas within both *Parachartergus* and *Pseudopolybia* nests of more than one type are built. The fusion of the three genera would only provide an artificial solution of the problems, since the wasps differ from one another in important points of structure.

1. *Parachartergus fraternus* (Gribodo, 1891).

This species has in the past been much confused with *P. apicalis* (Fab.), of which Ducke (1910 : 534) supposed it was a variety. Rarely, specimens occur which are in some respects intermediate, but it appears that the two species are essentially distinct and that in British Guiana only *P. fraternus* occurs (recorded from Guiana as *Chartergus apicalis* by Cameron, 1912).

Bequaert (1944 : 303) records the typical form of *P. fraternus* from Dutch Guiana : Paramaribo and the var. *concolor* (Gribodo, 1891), in which the wing-tips are transparent, not milky-white, with veins in this part brown, not yellow, from BRITISH GUIANA : Courentyne R., Hapseba; Arakaka. In the British Museum Collection there are specimens of the typical form from PANAMA : La Chorrera, ♀. BRITISH GUIANA : Yawakuri R., Cattle Trail Survey, vii.1919, 2 ♀ (*A. A. Abrahams*); North-west district, Issororo, viii.1919, 2 ♀ (*G. E. Bodkin*); Essequibo R., Moraballi Creek, clearing, 16.ix., trail, 17.ix., Wallaba Forest, 23.ix.1929, 3 ♀ (*Oxford Univ. Exped.*); New River, 700 ft., 10.i.1938, 17 ♀ (*C. A. Hudson*); Mazaruni R., second falls, 18.viii.1937, ♀ (*Richards and Smart*); Potaro R., Kaieteur Savannah, nest 235, 9.ix.1937, 140 ♀ (*Richards and Smart*); no precise locality, 2 ♀ (*J. Rodway and A. W. Bartlett*). DUTCH GUIANA : Surinam, 21 ♀ (*S. M. Klages*). BRAZIL : Barcellos

2.vii.1905, ♀ (*A. Ducke*); Pará, ♀; Itacoatiara, viii.1935, 22 ♀ (*G. V. Vredenburg*); one with 2 ♂ Strepsipterous puparia beneath tergite 5; little modification or distortion visible).

According to Ducke (1910) and Bequaert (1938), it is also found in Colombia, Venezuela, French Guiana, Peru and Bolivia. The variety *concolor* (Grib.) was recorded by Bequaert (1944) from French Guiana, Brazil, Trinidad, Colombia and Panama, as well as from British Guiana. In the British Museum collection are 18 ♀ from Brazil (including 1 ♀ Minas Geraes), Venezuela, Colombia and Panama.

Parachartergus apicalis (Fab.) seems mainly to be found in districts surrounding the area occupied by *P. fraternus*, though there is considerable overlap. In the British Museum collection are specimens from Mexico, British Honduras, Guatemala, Costa Rica, Colombia, French Guiana, S. Brazil, Paraguay. According to Ducke (1910), it is rare in Amazonia, and it appears to be commonest in Central America.

A large number of other insects exhibit the striking colour-pattern of these two wasps; the following have been recorded: *Mischocyttarus socialis* (Sauss.) (= *ater* of authors) and its var. *uniformis* Beq., *Polistes apicalis* Sauss., *Monobia apicalipennis* Sauss., *Odynerus subapicalis* Fox (Vespidæ); *Gorytes* sp. (Sphecoidea); *Odyneropsis apicalis* Ducke, *Chalaeopogonius moestus* Cress., *Tetrapedia maura* Cress. (Apoidea); *Leucospis leucotelus* Walk., *L. apicalis* Cress. (Chalcididae); *Seminota mexicana* Cress. a parasite of the nest of *P. apicalis* (Fab.) (Trigonaliidae); *Iphiaulax* sp. (Braconidae); *Ceriodes* sp. (Syrphidae); *Anyctes affinis* Rothschild, *A. anthracina* Walk., *Pompiliodes albomarginata* Druce, *P. aliena* Walk., *Pseudosphex strigosa* Druce (Symptomidae); *Aegeria* sp. (Aegeriidae); an Asilid predator on the wasp in Mexico is *Promachina trapezoidalis* (Bellardi) (Ducke, 1910: 460; Rothschild, 1922 and 1931; Poulton, 1931; Bequaert, 1938: 108; FitzGerald, 1939: 105).

Nearly all accounts of the biology have been ascribed, perhaps mostly correctly, to *P. apicalis* (Fab.), but Ducke (1910: fig. 16) illustrates the nest of *P. fraternus* (Grib.) from Pará. It does not appear that they differ in any of the details so far recorded, except that Ducke (1910: 536) states that *P. apicalis* is very aggressive, whereas we did not find this to be true of the colony of *P. fraternus*. The envelope, characteristically corrugated, is attached to a branch or large leaf, with an opening at the lower end. Inside, and quite free from it, is a number (5-7) of combs supported at right angles to the branch or leaf by a pillar from one edge.

In 1937 one nest, no. 235, was found on the underside of a dead leaf of the Bromeliad, *Brocchinia micrantha* (Baker) Mer, Kaieteur Savannah, 4.ix. (pl. 4, figs. 30-31). The nest was observed for two days but during the night of 6-7.ix. it was deserted and a new nest was started beneath another dead *Brocchinia* leaf, about 10 yards away. The wasps were busily engaged in eating away the old envelope, of which about one-third had already gone by 9.0 a.m. (pl. 4, fig. 32). The material was being used to build the new nest. At 10.30 a.m. on 7.ix. the cells of the old nest were found to be completely empty and clean, and on 9.ix. it was taken for preservation. It had almost certainly been raided by driver ants (Ecitoninae).

The old nest had seven combs with 7, 50, 87, 100, 79, 57 and 13 = 393 cells. The new nest was being made by rows of wasps building out new combs at

right angles to the leaf. By 10.30 a.m. seven combs had been started, many of the cells already containing eggs; the envelope was growing very fast. By 1.30 p.m. the top part of the envelope was 2.5 cm. high, tapering to nothing at the lowest comb. The wasps building the envelope sat along its edge with their heads upwards. In making the combs they scrambled about in all directions. All the cells now had eggs in them. A group of about 12 wasps, apparently sentries, sat on the leaf just below the lowest comb. Other wasps sat on the leaf between the combs, and apparently had a similar function or were perhaps building the buttresses attaching the combs to the leaf. Some of them may have been waiting for paper to be brought. The paper was carried by 2-4 individuals which were removing the old envelope, working on the shady side. They made a ball 2.0-3.0 mm. diameter, and on arrival, handed it over to another individual, perhaps one of the so-called sentries (pl. 4, fig. 33).

At 2.0 p.m. on 9.ix. the new envelope was complete except for the bottom 10.0 cm. or so. At 5.30 p.m. on 9.ix. it was noticed that no wasps were working on the old nest but they were found sitting all round the new one on the *Brocchinia* leaves. The new nest had been invaded by small ants (undetermined ECTONINAE). The wasps were making no sort of resistance, and in 10 minutes all the ants were gone, leaving the cells empty. The wasps were beginning to return, but 119 were captured. At 6.0 a.m., 10.ix., another 21 were found on the nest, and this was probably the complete colony. The nest was now taken and all the cells were found to be empty. There were seven combs with 14, 20, 28, 26, 35, 28 and 16 = 167 cells.

One hundred wasps were dissected; 16 were queens, with 1-10, mean 7.1 eggs, and 84 were workers. There were thus probably 22 queens and 118 workers in the whole nest. There were no intermediates.

The envelope has very characteristic corrugations. The carton is tough and elastic, with a fibrous structure, much as in *Protopolybia*. The cells were 4.5 mm. in diameter and 8.0 mm. deep. The wing-length and hamuli numbers were measured in 11 ♀ and 20 ♂. The means were 11.32, 11.13 mm., and 10.1, 9.85, respectively. The differences are not significant.

2. *Parachartergus griseus* (Fox, 1898).

Bequaert (1938 : 109), following Ducke (1910 : 533), recognised five varieties of *P. fulgidipennis* (Sauss.), but he knew three of the forms, including the typical *P. fulgidipennis*, only from descriptions. The British Museum collection includes all the forms not seen by Bequaert, and it seems that in reality three species are involved, which, very briefly, may be separated as follows: (1) *P. fulgidipennis* (Sauss.) (type in coll. B.M.). Size rather small; malar space at narrowest not longer than half width of antennal socket; propodeum with strongly prominent, rounded lateral lobes. Colour largely ferruginous. (2) *P. griseus* (Fox) = *bentobuenoi* R. von Iher.). Like *P. fulgidipennis* (Sauss.), but tergite 1 more strongly punctured and more shining; lateral lobes of propodeum considerably less strongly produced dorsally; colour mainly dark grey. The var. *fasciipennis* (Ducke), which we have not seen, is a form of this species, according to Bequaert. (3) *P. amazonensis* Ducke, 1905. Larger than *P. fulgidipennis* (Sauss.); pro- and mesonotum somewhat more sparsely and shallowly punctured; malar space at narrowest at least as

wide as antennal socket; lateral lobes of propodeum more produced than in *P. griseus* (Fox), but less than in *P. fulgidipennis* (Sauss.). Colour testaceous, with a creamy band on the hyaline wings. The variety *flavofasciatus* (Cameron, 1906) probably belongs here. The disc of the mesonotum and scutellum and tergites 2-6 are black. The fore-wings are blackish with a central yellowish band. It seems to be rather larger than typical *P. amazonensis* Ducke.

Bequaert (1944 : 303) records typical *P. griseus* from BRITISH GUIANA : Moraballi Creek, Brazil and Peru. In the British Museum collection are the following specimens :—BRITISH GUIANA : Kartabo, viii.1922, 1 ♀ (*M. D. Haviland*); Essequibo R., Moraballi Creek, nest 1599, 5.ix.1929, 9 ♀ (*Oxford Univ. Exped.*); no precise locality, type of *Chartergus trichosomus* Cameron, 1912, 1 ♀, also 1 ♀ (*J. Rodway*). BRAZIL : Ega, 1 ♀; Upper Amazon, 1 ♀; R. Mapura (Trombetas), 12.xii.1907, 1 ♀ (*Ducke*).

The variety *fasciipennis* Ducke was recorded by Bequaert from BRITISH GUIANA : Ite Cattle Trail, and was originally described from Brazil.

According to Ducke (1910 : 533), the nest of typical *P. fulgidipennis* (Sauss.) resembles that of *Leipomeles*, the envelope covering the underside of the leaf and enclosing several small combs, each on its own pillar. Unlike *Leipomeles*, however, the envelope is not made to imitate the leaf-surface, but is green owing to a covering of moss fragments. A nest of *P. amazonensis* Ducke had a plain, greyish-testaceous envelope.

The nest of *P. griseus* at Moraballi Creek was beneath the leaf of a *Morabukea* (*Mora gonggripui* (Kleinh.)), 6 ft. from the ground, in dark forest. The laurel-like leaf was 20.0 cm. long and 7.5 cm. broad, and the envelope was 13.7 cm. long, starting about 2.5 cm. from the base of the leaf, and followed the edge of the leaf till near the tip, where the edges of the envelope converged on to the disc of the leaf. The entrance was a flat slit at the point nearest to the leaf-tip. The envelope was thin and semi-transparent (thicker towards the base of the leaf), pale greenish outside, white inside. Beneath it was a single comb of 316 cells (5.6×3.7 cm.) suspended from the mid-vein by a pillar 6.0 mm. thick, and by a much thinner one near the base of the leaf. The cells were white and about 8.0 mm. long. A large central area of cells contained cocoons, surrounded by larvae and then eggs. Only ten wasps were recovered and they were very tame. R. von Ihering (1904 : 239, pl. 5, fig. 2, as *P. bentobuenoi*) describes a rather similar nest from the R. Juruá. The comb, however, was supported by many pillars, and the envelope was covered with chewed moss. The cells were 9.0×3.6 mm.

3. *Parachartergus smithii* (de Saussure, 1854).

The only record of this species from BRITISH GUIANA appears to be that of Bequaert (1944 : 303), from Kartabo. It is also known from BRITISH HONDURAS, COSTA RICA, COLUMBIA, ECUADOR, PERU and BRAZIL. The nest is unknown.

4. *Parachartergus frontalis* (Fabricius [1805]).

This species is recorded by Ducke (1910 : 333), from BRAZIL, AMAZONIAN PERU, and VENEZUELA but not previously from British Guiana. In the British Museum collection, besides specimens from Panama (Bugaba, 23 ♀), Brazil and Peru, is one male, BRITISH GUIANA : Essequibo R., Moraballi

Creek, dark forest, 25.ix.1929 (*Oxford Univ. Exped.*). The male differs from the female as follows :

Clypeus less produced with silvery pubescence ; tempora narrower ; bristle on labial palp very weak ; antennae simple, of 13 segments ; sternite 7 flat ; antennae with segments 1 and 3-13 ferruginous beneath ; clypeus to just above antennae, centre of ocular sinus, and outer orbits yellow ; spot on propisternum and pronotal keel and hind margin more extensively yellow ; scutellum black, postscutellum yellow, streak on dorsal half of mesopleuron yellow ; fore coxae beneath, spot on hind coxae, fore femora beneath, antero-distal mark on mid femora, fore tibiae anteriorly, yellow.

The nest (Moebius, 1856 : 23, pl. 14) is constructed beneath a leaf ; a streaky grey envelope covers a flat comb suspended from the mid-rib by a single pillar.

16. *Pseudopolybia* Saussure, 1863.

This genus consists of five species, found in various parts of rain forest from Central America to South Brazil. Three of the species have been found in British Guiana.

The nests of three of the species are calyptodomus, stelocytтарous and rectinidal, that is essentially like *Stelopolybia pallens* (Lep.), though the entrance is not at the end of a tube-like extension, and the envelope consists of a number of layers. *P. pusilla* (Ducke), of which the nest is here described for the first time, makes a nest like *Leipomeles* Moeb. The nest of *P. langi* J. Beq. has not been described.

1. *Pseudopolybia difficilis* (Ducke, 1905).

This species, which is superficially very like *Stelopolybia fulvo-fasciata* (Deg.), is recorded by Bequaert (1944 : 299) from BRITISH GUIANA : Source of Essequibo R., and it is also known from Brazil, Peru and Bolivia.

The nest has been described and figured by Ducke (1910 : 528, fig. 13).

2. *Pseudopolybia langi* J. Bequaert, 1944.

Bequaert described this species from BRITISH GUIANA : Kamakusa from nest material but the nest itself was not described.

3. *Pseudopolybia pusilla* (Ducke, 1904).

Cameron (1912) described this species from British Guiana as *Polybia spilogastra* ; according to two females marked as types in the British Museum collection, Bequaert was incorrect in synonymising Cameron's species with *Leipomeles dorsata* (Fab.), though it superficially resembles that species. On the Oxford University Expedition to British Guiana, Mr. J. E. Duffield found a nest on the banks of the Essequibo R., Monkey Jump, 9.x.1929, and about 60 ♀ are preserved. Apart from these Guiana records, the species is only known from BRAZIL : Pará and Oyapoc.

According to Mr. Duffield's notes the nest was beneath a laurel-like leaf, 4 ft. from the ground, in a small clearing in dark forest. The chocolate-brown carton envelope extended over the whole under-surface of the leaf, including the tip, beneath which was the exit-hole. Inside were nine small groups of from 9-90 cells, each suspended from its own petiole, about 1 cm. long. The centre of the envelope was about 2.5 cm. below the leaf surface. About 100 wasps were present.

17. *Leipomeles* Moebius, 1856.

The single species of this genus carries still further the reduction in the number of palp-segments shown in *Pseudopolybia* Sauss.

1. *Leipomeles dorsata* (Fabricius [1805]).

Fabricius described the species from the Essequibo R., and Cameron (1912) described it as *Polybia sulciscutis* from British Guiana (2 ♀ in coll., British Museum, both marked as types). Bequaert (1944:304) records it from BRITISH GUIANA: Source of Essequibo R.; Essequibo R., Monkey Jump. In the British Museum are the following Guiana specimens: Monkey Jump ex nest, 11.x.1929 (*Oxford Univ. Exped.*); Essequibo R., Moraballi Creek, ex nest, 25.ix.1929 (*Oxford Univ. Exped.*); Kartabo, vi.1922, 2 ♀ (*M. D. Haviland*); Kutari Sources, 10.i.—10.ii.1936, ♀ (*G. A. Hudson*); Makauria R., 22.ix.1937, ♀ (*Richards and Smart*). Outside British Guiana it is recorded from Dutch and Brazilian Guiana, Amazonia, Bolivia, Peru, Ecuador and Panama.

The nest has been described and figured by Moebius (1856:26, pl. 17), R. von Ihering (1904:246, pl. 6, fig. 8), Ducke (1905b:675, pl. 2, fig. 6) and (1910:536, fig. 17), Williams (1928:154, pl. 29, fig. 221). According to Ducke and Williams, the wasps put some sticky material on the petiole of the leaf to which the nest is attached and this is supposed to act as an ant-guard. The envelope may be grey, brown or green, owing to the incorporation of moss fragments. Markings on the surface are said, sometimes, to imitate the veins. Attached to the leaf is a number of small combs, each with its own petiole. When the nest grows, these may fuse to form a single comb supported by several pillars.

Nest 2864, Moraballi Creek, 25.ix., was attached beneath the leaflet of a young palm, the edges of the leaflet being somewhat drawn together. The envelope was 11.0 × 6.0 cm., semi-transparent white, with numerous elongate black dots. The exit-hole, 5.0 × 3.0 mm., was at the base of the leaf. There were nine separate groups of cells, each hung from its own petiole; the biggest consisted of 50 cells, the smallest of two cells in the process of construction. About half the cells of the larger groups contained cocoons which were unusually large, projecting 2.0–5.0 mm. beyond the cells, which they equalled in length. Nearly all the wasps were lost.

18. *Mischocyttarus* de Saussure, 1853.

This, the largest genus in the POLYBIINAE, was revised by Richards (1945). In that paper 68 species were recognised but a number more described in the literature are probably also distinct, and undescribed ones have been seen in more recent collections. Bequaert (1944:261) lists 21 species from BRITISH GUIANA; in view of these recent papers it is only necessary to list the species here. The following 18 species are listed in both papers:—*M. labiatus* (Fab.), *M. smithii* Sauss., *M. rotundicollis* (Cam.), *M. flavicans* (Fab.), *M. carbonarius* (Sauss.), *M. heliconius* Rich., *M. metathoracicus* (Sauss.), *M. injucundus* (Sauss.) var. *bimarginatus* (Cam.), *M. lecointei* (Ducke) and its var. *guianensis* Rich., *M. metoecus* Rich., *M. foveatus* Rich., *M. collarellus* Rich., *M. superus* Rich.,

M. prominulus Rich., *M. surinamensis* (Sauss.) var. *occidentalis* Rich., *M. cerberus* (Ducke) var. *acheron* Rich., *M. oecothrix* Rich., *M. synoecus* Rich.

M. sylvestris Rich. is probably a variety of *M. lemoulti* (R. du Buysson, 1908) and has been recorded under both names. Richards (1945) also records *M. drewseni* Sauss. and its var. *steinbachi* Rich., *M. alfkenii* (Ducke) var. *trinitatis* Rich. Bequaert (1944) records two species not noted from British Guiana by Richards, viz., *M. collaris* (Ducke) and *M. duckei* (R. du Buyss.).

The species of *Mischocyttarus* build small stalked uncovered combs (stelocytarus, gymnodomous), rarely of more than 50 cells in Guiana, but occasionally with 2-400 cells in S. Brazil. Most nests are inhabited by one queen and a few workers; in Guiana rarely by more than ten wasps. There is evidence that two queens at least occur in some colonies, and nests may be founded by a single queen or by a queen and one or two workers. The difference between *Mischocyttarus* and the normal pleometrotic swarming Polybiines is much more in the size of the colony than in the method of foundation or in the number of queens. Many nests of *Polybia* have only one queen. Certain aspects of the biology of the genus are discussed further on p. 116. Reid (1942) has described the larvae of eleven species of *Mischocyttarus*. They have characteristic ventral thoracic lobes and, sometimes, a clothing of bristles.

20. *Coloboclypeus* Brèthes, 1926.

This remarkable genus contains, so far, one species described from Colombia, but I understand that Dr. Bequaert has seen another from Peru. In his key (1944 : 252), it would probably run to couplets 10 or 11, and would be distinguished by the bidentate clypeus and flat, truncate propodeum.

21. *Polistes* Latreille, 1802.

This large and cosmopolitan genus is usually placed in a different subfamily (POLISTINÆ) from the Polybiines. It appears, however, somewhat doubtful whether the structure of the adults is sufficiently distinct to warrant this, and the larvae, of which Reid (1942 : 299) has described three species, are more like those of the ordinary POLYBIINÆ than are those of *Mischocyttarus*.

The classification of the species depends in the first place on the arrangement of the sutures of the mesopleuron. In describing these Bequaert (1937, etc.) has used a terminology which, we believe, differs from the one usually employed in the order. What he terms the "prepectal suture" is an epicnemial suture. His "median episternal groove" is what marks off the prepectus.¹⁶ The mesopleural suture is probably indicated above the punctiform fovea but, as in most higher Aculeates, it is coincident below with the meso-metapleural suture. When the thorax of *Polistes gallicus* (L.) is examined from the inside, the epicnemial groove is invisible; it is purely superficial and external. The prepectal suture is marked by a strong invaginated keel. This agrees with its importance in the classification of the Hymenoptera and the longer evolutionary history behind it. It is, however, uncertain whether the prepectal sutures of all Hymenoptera are homologous. The pleural suture below is certainly coincident with the meso-metapleural suture; above, it is very

¹⁶ According to Snodgrass (1935 : 184) a part cut off in front of the mesepisternum is a pre-episternum; if it also includes a sternal element it is a prepectus.

feebly marked internally but, judging from the position it occupies, it is probably correctly identified.

In habits, the species of *Polistes* resemble *Mischocyttarus* and make similar small, stalked, uncovered combs, though rarely of the peculiar shapes which are found in some species of that genus. Most colonies consist of a single queen and a relatively small number of workers, but more than one queen may be present (p. 106), especially in the early stages of the colony, and foundation may be by swarming (p. 5), especially in the tropics.

Four of the species recorded by Bequaert (1944) from British Guiana, viz. *P. subsericeus* H. de Saussure, 1854, *P. occipitalis* Ducke, 1904, *P. melanosoma* H. de Saussure, 1853, *P. deceptor* Schulz, 1905, are not represented by British Guiana specimens in any of the collections we have examined, and they will not be referred to again. On the other hand, we include two species on which we made some observations in the West Indian islands, and some notes on African species are included in Appendix 3. The specimens on which Cameron (1912) based his records of *P. rubiginosus* Lep. and *P. instabilis* Sauss. have not been traced.

1. *Polistes pacificus* Fabricius [1805].

This species was recorded from British Guiana by Cameron (1912) and Bodkin (1917), but no specimens were seen by Bequaert (1944) though he knew it from adjacent countries. There are specimens of the typical form (in the sense of Bequaert, 1937 : 196) in the collection of the BRITISH GUIANA Dept. Agric. : Essequibo R., Onderneeming, 18.iv.1915, ♀ (*G. E. Bodkin*). The Oxford University Expedition also obtained one female—Cuyuni R., xi.1929.

The nest of the typical form of the species at Belem do Pará has been described by Ducke (1905b : 693, pl. 4, fig. 27) and by Schulz (1905 : 117). The colonies there were very small, usually attended by a single female, and the comb had a long stalk. Myers (1935 : 13) and FitzGerald (1938 : 181) have described nests of what was probably the same form in Trinidad. According to FitzGerald, it is there characteristic of second-growth forest. Myers found one small nest of about 6 cells attached to the carton of a nest of the tree-ant, *Azteca chartifex* Forel ; a nest of *Nasutitermes* sp. was more or less combined with that of the ant. FitzGerald bred an Encyrtid, *Signiphora polistomyiella* Rich., from a Dipterous parasite of the larva, and found a colony of 12 lethargic wasps which was each parasitised by a Strepsipteron. A dark variety of the wasp (presumably the var. *trinitatis* Bequaert, 1937) resembles in colour *Polybia striata* (Fab.) (*sycophanta* Grib.) (FitzGerald, 1938, 1939). Nests of the var. *actaeon* Hal. (= *limai* R. von Ihering, 1903a) have been described by Curtis (1844), R. von Ihering (1903a ; 1904 : 241, pl. 5; fig. 3) and Bertoni (1918). The colonies again seem to be small. According to Bertoni, the carton is covered with black varnish, and von Ihering states that the cells are 5.0 × 17.0–18.0 mm. Dover (1924) quotes the opinion of C. Allen, that the species flies mainly after dusk, but this needs confirmation.

2. *Polistes guyanensis* Cameron, 1912.

After much study, it seems that this is a distinct species allied to *P. pacificus* Fab. It has an epicnemial suture, but the prepectal suture is very

weak and in the lower half indicated as much by colour as by an impressed line. The clypeus is a little more produced though its centre is blunter than in *P. pacificus*, but less than in *P. ruficornis* Sauss. The malar space is clearly shorter than in *P. ruficornis*. It will not run to any species in Bequaert's key (1937:173) to the species of the group of *P. gallicus* (L.), and should probably be referred to his group of *P. bicolor* Lep. In this group it is especially distinguished by having a groove separating (for the anterior three-fifths) the metapleuron from the metasternum; this groove is absent in *P. melanosome* Sauss., *P. bicolor* Lep., and *P. deceptor* Schulz, is faintly indicated in *P. occipitalis* Ducke and shown in the anterior half in *P. pacificus* Fab., *P. cinerascens* Sauss., and *P. ruficornis* Sauss. The 1st abdominal tergite in profile has a much more gentle slope than in *P. ruficornis*, *P. cinerascens* or *P. pacificus*. In the type, the mandibular teeth are very blunt, but this may be an abnormality or due to wear.

It is possible that it is really more allied to *P. subsericeus* Sauss. (group of *P. gallicus* (L.)) which also has a nearly complete metasternal groove, but the tempora are broader and the occipital keel descends further. The following is a description of the colour-pattern.

Female. Reddish-brown; vertex to top sixth of clypeus (except small orange spots just above antennae and inner orbits), spot in front of pronotal collar, and suffused disc of mesonotum, black. The following parts are yellow: inner orbits from above ocular sinus to clypeus, upper part of sides of clypeus, whole outer orbits, two central spots on anterior margin of pronotum, its ventral angles, its collar and narrow posterior margin, two abbreviated lines on disc of mesonotum, anterior third of scutellum and whole of its axillae, anterior half of postsutellum, small propodeal spots near spiracles, very broad bands on each side of furrow, valves and orifice, triangular spot at top of prepectus, spot at top of metapleuron, large areas on all coxae, small spot at tip of all femora, very narrow bands on abdominal tergites 1-4. Wings pale yellow-brown, considerably darkened along costa. Tegulae testaceous. Length of fore-wing 11.0 mm., hamuli 13.

Male. Prepectal suture hardly traceable; malar space much shorter than in *P. ruficornis* Sauss.; antennal segment 13 a little curved (unlike *P. pacificus* (Fab.); clypeus in contact with eye for a distance at least two-thirds length of malar space, ventral margin projecting further than in *P. pacificus*, less than in *P. cinerascens* Sauss.; metasternal furrow as in female. Base of abdomen damaged so that the shape of the 1st tergite cannot be verified. Much of head, thorax and abdomen (here browner), black; mandibles, suffusion at ventral margin of clypeus, flagellum beneath, postero-lateral aspect of pronotum, spot at bottom of metapleuron, large lateral areas on the propodeum, suffusion beneath abdomen, legs (except black dorsal and ventral black stripes on coxae and femora) ferruginous. Narrow sides of clypeus, narrow margin from just above ocular sinus to top of clypeus, narrow outer orbits, scape beneath, narrow anterior and posterior margins and keel of pronotum, anterior third and axillae of scutellum, anterior half and axillae of postsutellum, moderate stripes on each side of furrow and valves and orifice of propodeum, narrow posterior bands of abdominal tergites 1-4, antero-dorsal stripes on coxae, yellow. Tegulae testaceous, inner margin yellow. Wings reddish-brown tinged, especially along costa, veins dark brown, disc of pterostigma orange. Length of fore-wing 9.5 mm., hamuli 12.

Specimens examined:—BRITISH GUIANA: Potaro Valley, v.1900, type ♀ and ♀ labelled "*P. pacificus*" (Cameron coll.); Cattle Trail Survey, Takaruni R., vi.1919, ♀ (*A. A. Abrahams*); North-west district, Issororo, ♂ (*C. B. Williams*).

It is probable that the male corresponds to the females. The second female in the Cameron coll. is darker than the type, and has the prepectal furrow even weaker; the black areas cover most of the head, except the mandibles but including the top of the clypeus; a larger area in front of the frontal keel, whole mesonotum, a suffusion of the scutellum and postscutellum, mesosternum in front of epicnemial furrow and abdominal segments 3-6. The yellow is confined to a U-shaped ventral area on the clypeus and the malar space. Dr. Bequaert has seen the specimen and considers that it belongs to *P. ruficornis* Sauss., but the metasternal groove and the flattened 1st abdominal tergite agree with the present species. The female from Takaruni R. also has a black mesonotum, but the pale markings are otherwise more extensive than in the type. The malar space is rather longer, as in *P. ruficornis*, but the metasternal groove and 1st abdominal segment differ from that species.

No other specimens seem to be known and the nest is undescribed; more material will be required to place it satisfactorily.

3. *Polistes ruficornis* de Saussure, 1853.

Bequaert (1944 : 259) has recorded the var. *demeraraensis* Bequaert, 1937 from BRITISH GUIANA :—Demerara, Mahaica R.; Georgetown; Blairmont. It was recorded by Bodkin (1917) under the name *P. crinitus* Felton (in part), and there is a female, Georgetown Botanic Garden, 14.ii.1918 (*G. E. Bodkin*) in the collection of the British Guiana Dept. Agric.

Strand (1912 : 325, pl. 9, fig. 3) describes the nest of the typical form of the species in Paraguay. It was on a dry plant twig about 40.0 cm. above the ground, and resembled that of *P. pacificus* var. *actaeon* (= *limai*) except that the petiole was parallel to the cells and shorter. The comb was 30-40 mm. long, 25-30 mm. broad, and 20.0 mm. deep. The largest cells were 25.0 × 5.0 mm., and the petiole was 5-6 mm. long and 1.8-2.0 mm. in diameter.

4. *Polistes versicolor* (Olivier, 1791).

This common S. American species was recorded from BRITISH GUIANA by Bodkin (1917) and, as vars. *versicolor* (Oliv.), *vulgaris* Bequaert, 1934, and *kaieteurensis* Bequaert, 1934, by Bequaert (1944 : 258). The first two are the ordinary forms in the seaward half of the country, the following specimens having been examined: var. *versicolor*, Essequibo R., Onderneeming, 13.xii.1914, 2 ♀ (*G. E. Bodkin*) (one det. as *P. crinitus* Felton in coll. British Guiana Dept. Agric.); Demerara, Plantation Uitvlugt, 27.iv.1912, ♀ (*G. E. Bodkin*); Berbice R., Plantation Providence, 19.ix.1913 (*G. E. Bodkin*); no precise locality, 2 ♀ (*Rodway, Bartlett*). Var. *vulgaris* Beq., Pomaroon R., 29.x.1913, ♀ (*G. E. Bodkin*); var. *kaieteurensis* Beq., Kaieteur Savannah, 2.ix.1937, ♀ (*Richards and Smart*).

The last-recorded variety is only known from Kaieteur. The species occurs in a great many other "varieties," revised by Bequaert (1933a), and the nests of some of them have been described and illustrations are given by de Saussure (1853 : pl. 8, fig. 6a) and Rau (1933 : 113, fig. 54). R. von Ihering (1903a : 1904 : 241, 282) observed the species in São Paulo, where it makes some of the largest nests seen in the genus, up to 22.0 cm. long, though regularly 5.5 cm. broad. The shape is irregular, rounded, elongate or lozenge-shaped,

with the petiole always completely excentric, short and thick. The cells were 6.0×20.0 – 23.0 mm. He notes that Saussure's figure is of an abnormal nest with a central petiole. As soon as the cells are 2.5 – 3.0 mm. long, eggs are laid in them, though they may develop very slowly at low temperatures.

The nest increases in size as the generations succeed one another, males appearing last and soon disappearing. The rest of the colony, however, may continue through the winter. Thus, on 18.vi.1903, a large nest was found with 289 inhabitants. No males were present and there was no brood in the cells, most of which contained a little honey. The colony was leading an idle life, and later the nest was abandoned. Apparently, in S. Brazil, females and workers often hibernate on the old nest or in some special refuge, as recorded by H. von Ihering (1896a : 450) at Rio Grande do Sul.

Nests in Paraguay, where they are sometimes common on bushes, have been described by Schrottky (1904) and Bertoni (1911). Many of the combs were long and narrow and, if not in a protected situation, are built so that the dorsal side of the comb is directed to the side from which most rain comes. In one nest the orientation of the cells was altered half-way along a comb so that half of them pointed in a reversed direction. In some years parasites (see below) were very destructive. In Trinidad FitzGerald (1938 : 182) found that colonies could be founded either by single females (1 ♀ on 16 cells with very young larvae) or by a swarm (10 wasps on a new comb of 4 cells). He also found one swarm, sitting on a root—a typical nesting site. It consisted of 12 females, 8 of which had developed ovaries. Schulz (1904 : 787), at Pará, found nests on shrubs and bushes by the roadside, especially beneath banana leaves ; also under beams in deserted mud huts. Even in this tropical region he found that breeding was interrupted during the rainy season, but the nests are apparently much smaller than those further south. They were heavily parasitised by an Ichneumonid. In Panama, Rau (1938 : 112) came to the conclusion that there was no seasonal cycle in breeding. Most of the nests were rather small, rarely as many as 70–90 cells. The combs were built under *Heliconia* leaves or under eaves, the petiole always being excentric. He gives evidence that colonies may be founded either by single females, or by small swarms and, possibly, by associations. He found one worker preying on a caterpillar.

Brauns (1905) described the Ichneumonid, *Mesostenus iheringi*, bred from this species by von Ihering, at São Paulo, and Bertoni (1911 : 100) found the same parasite abundant in Paraguay, together with the Trigonalid, *Seminota marginata* Westw. Brèthes (1923 : 6) described the Strepsipteron, *Xenos bonariensis*, from this *Polistes* in Buenos Aires.

5. *Polistes testaceicolor* Bequaert, 1937.

Polistes analis Fabricius, 1798 nec 1775.

According to Bodkin (1917), this species is fairly common in the interior of BRITISH GUIANA, and Bequaert (1944 : 259) records it from Bartica, Georgetown, Warina (North-west district), Tumatumari, Kaieteur, Mt. Everard, and Arakaka. In the British Museum collection are 7 ♂, 10 ♀ from localities mostly near Kartabo. It seems to occur more in forest than in open places, and has a close colour resemblance to *Stelopolybia testacea* (Fab.), which often

occurs in similar situations. Outside the Guianas, it is found from Costa Rica to Amazonia, Peru and Bolivia. According to Bequaert, it is often heavily stylipised.

6. *Polistes erythrogaster* Ducke.

The typical form of this species, which is mainly black with a dark red-brown abdomen, was recorded by Bequaert (1944 : 259) from Mt. Roraima. The two specimens which we have seen, though structurally similar as pointed out by Dr. Bequaert, belong to undescribed colour varieties.

Var. *moraballi* var. n.

♀. Testaceous, somewhat yellow variegated. Mid and hind coxae with ventral and dorsal blackish streaks; abdomen with posterior margins of tergites 1 and 2, spots on sternites 1 and 2, and whole of tergites and sternites 3-6, black. Wings hyaline, costa of fore-wing strongly amber-tinged. Length of fore-wing 16.0 mm., hamuli 17.

Exactly like *P. testaceicolor* Beq. in colour, but microsculpture of clypeus more distinctly punctate; pronotal keel stronger, with a small angular hump in centre, and sides more strongly lobate, no pronotal fovea (present in *P. testaceicolor*); tempora narrower than eye, chiefly because the latter is somewhat swollen below, temporal keel stronger; especially below. Antennal socket separated from eye by its own width (not by more). Inter-antennal prominence without the central groove present in typical *P. erythrogaster* and in *P. testaceicolor*.

Type ♀, BRITISH GUIANA: Essequibo R., Moraballi Creek, no. 2516, ix.1937 (*Oxford Univ. Exped.*).

Var. *angulinus* var. n.

♀. Black; outer orbits narrowly, inner orbits from clypeus to ocular sinus, pale yellow; some reddish suffusion on ventral half of clypeus, at ventral corners and around centre of posterior margin of pronotum, on propodeum, on fore tibiae and on last segment of fore and mid tarsi. Antennae with segments 4-12 dark reddish-brown. Wings yellowish brown, especially along costa. Length of fore-wing 17.0 mm., hamuli 19. Supra-antennal prominence with rather distinct groove.

Type ♀, BRITISH GUIANA: Potaro R., Tukeit trail, nest 189, 4.xi.1937 (*Richards and Smart*).

Structurally identical with the typical form, but in colour closely resembling *Stelopolybia angulata* (Fab.) and several homiochromic species of *Polistes*.

It differs from *Polistes melanosoma* Saussure in lacking the kink in the temporal keel, in lacking the pronotal fovea, in having the pronotal keel stronger, especially at the sides and raised into a hump in the centre; the antennal sockets are nearer to the eyes and the malar space is a little shorter.

In the British Museum collection is a male labelled "*Polistes deceptor* Schulz type, Surinam (*Fruhstorfer*).". This cannot be the real type but may be a paratype, though it seems to differ from what Bequaert calls *P. deceptor*, for the head is not much swollen, differing in this respect markedly from *P. bicolor* Lep. This Surinam species is close to the var. *angulinus* but the pronotal keel is weaker, not humped in the centre, and more obtuse at the sides, especially near the fovea which is present.

The single female of the variety *angulinus* was found on her nest beneath the leaf of a small shrub, about 4 ft. from the ground. The trail here runs

down the escarpment, and the forest is of an intermediate type, less dark than the normal tall forest. Both the wasp and its nest were very like those of *Mischocyttarus carbonarius* (Sauss.) which occurred nearby, and for which it was mistaken at the time. Only one wasp was present, and there were 6 shallow cells (4.0 mm. deep), all containing eggs. The carton was pale brown and fibrous.

7. *Polistes goeldii* Ducke, 1904.

This species is included by Bequaert in his key (1944 : 255) but is recorded from BRITISH GUIANA only by Bodkin (1917 : 306), who says that it is rare in the interior of the country. We have seen a female : Tumatumari, xii.1915 (G. E. Bodkin—British Guiana Dept. Agric.).

Ducke (1904 : 368, pl. 1, fig. 6), who described the species from the Amazonian region, notes its resemblance in colour to *Synoeca surinama* (L.). The comb is a remarkable structure, only 2 cells wide but up to 20 cells long. It is attached to trees or shrubs.

8. *Polistes carnifex* (Fabricius, 1775).

Bequaert (1944 : 255) includes this species in his key, though it has been recorded from British Guiana only by Cameron (1912). We found two nests of the typical colour-form, in the sense of Bequaert (1936), on the Kaieteur Savannah, where both were conspicuous in their natural surroundings.

Nest 157, beneath leaf of the Bromeliad, *Brocchinia micrantha*, 3 ft. from ground, open situation, 2.ix. It consisted of a comb of 25 cells, containing 14 eggs, 7 larvae and 1 cocoon; 3 were empty. There were two wasps, which were not dissected.

Nest 161, beneath leaf of *Clusia* sp., 3 ft. from ground, open situation, 3.ix. (pl. 4, figs. 34–36). There were 87 cells, with 7 empty, 32 eggs, 28 larvae and 20 cocoons. The 9 wasps consisted of 1 queen, 4 workers and 4 males. The workers had their ovaries partially developed, but no eggs were ripe. The nests were of silvery-grey carton, thin in places but of a rigid fibrous texture. The cells were 8.0 mm. in diameter and 35.0 mm. long. The cocoon caps were attached either at the distal margin of the cell, or, where one side of the cell was higher than the other, 1.0–3.0 mm. below it. They were only slightly domed in the centre. The external surface of the comb was varnished near the central petiole. R. von Ihering (1904 : 240) gives a very similar description of the nests at São Paulo, where more than 30 cells are rarely built. The largest nest of the var. *ochreatea* Spin. found by FitzGerald (1938) in Trinidad had 59 cells. Bequaert (1936 : 380) describes a nest which he found at Puerto Castilla, Rep.-Honduras. There were two similar-looking wasps, probably both queens; 19 cells, 3 capped, 5 open with larvae, and 11 with eggs. He notes that the cocoon-cap is not convex and lies a little below the rim of the cells. There are several records of stylopised specimens. The nest has also been figured by de Saussure (1852 : Pl. 10, fig. 5).

9. *Polistes canadensis* (Linnaeus, 1758).

The typical form and the var. *infuscatus* Lepeletier, 1836 (= *amazonicus* Schulz, 1905) are both recorded from British Guiana by Bequaert (1944 : 260). The *Polistes urceolata* Erichson, 1848, described from British Guiana, belongs

to one of these forms. According to Bodkin (1917 : 306), it is the commonest species in the colony, and he gives some account of its biology. It seems to occur chiefly on the coastlands, but also turns up in the more open places in the interior (e.g. on the top of Mt. Roraima). We had no opportunity of studying its habits in British Guiana, but we made observations on the var. *cinctus* Lepeletier, 1836, in St. Vincent. This form, according to specimens in the collection of the British Museum, is found on the islands of St. Vincent, Barbados and Moustique (Grenadines), while, according to Bequaert (1943c : 118), it is also found on Martinique and St. Kitts, and introduced into St. Lucia and Montserrat. We found it nesting commonly on an earthen bank overhanging the road at King's Hill Diamond Estate. Some were attached to the earth and others to roots (pl. 4, fig. 37). Five colonies were studied. Many cells in old deserted nests were occupied by the solitary wasp, *Pachodynerus quadripennis* (Sauss.).

Nest 356. On a root, 10 ft. up, 8.x. There were about 50 cells. Two areas of comb contained pupae and two larvae, and the part furthest from the petiole consisted of shallow cells containing eggs. There were also a few eggs in cells near the petiole, presumably a second laying in these cells. Several wasps returned to the site after the nest was taken and these were captured. There was 1 queen, with 35 ovarian eggs, 13 workers and 9 intermediates. The ovarian development of workers and intermediates intergraded completely.

Nest 357 was a similar nest with the same data. Eggs, larvae and pupae were dispersed throughout the comb but the area furthest from the petiole consisted of shallow cells with eggs only. It was evidently a rather more mature colony. Many wasps returned to the site after the nest had been taken, and 24 were captured in all. There were 1 queen (26 ovarian eggs), 1 ♂, 13 workers and 9 intermediates. The intermediates intergraded with the workers very nearly completely; none of them contained any ripe eggs.

No. 358 (nest with the same data) was not taken, but 18 wasps were captured and dissected. They consisted of 1 queen (30 ovarian eggs), 7 ♀ and 10 intermediates, the two latter groups intergrading.

No. 359 (nest with same data) was a smaller nest with 25 cells, containing 12 eggs, 6 larvae and 4 pupae. Only 2 wasps returned later to the site. The 6 wasps captured consisted of 1 queen (22 ovarian eggs) and 5 workers or intermediates with many egg-rudiments partly developed but none ripe.

No. 371. Found on the same site, 31.vii., had 27 cells, all with eggs, and 9 wasps which were not dissected.

The nests were made of grey or pale brownish fibrous carton, and the completed cells were 5.0 mm. in diameter and 15.0 mm. deep. The cocoon-caps were well domed but did not project much beyond the distal ends of the cells.

A study was made of the wing-lengths and hamuli numbers of 4 ♀; 33 ♀ and 33 intermediates.¹⁷ The figures are given in Table 23. It will be noticed that the hamuli numbers in the intermediates look as if they might be bimodal. This might be because they consist of a mixture of young queens and of workers with partly developed ovaries.

Some account of this variety in the islands is given by Ballou (1915, 1934 : as *Polistes annularis*). On St. Vincent it controlled the cotton-worm, *Alabama*

¹⁷ The 5 specimens from nest 359, which might have been either workers or intermediates, were classified as the latter on their wing characters.

argillacea Hb., to such an extent that for 10 years Paris green and other insecticides were not used. It is similarly abundant on Barbados. Attempts in 1910 and subsequent years to establish it on Montserrat, St. Lucia and Antigua, to control the same pest, were ineffective, probably because of the destruction caused by the Pyralidid moth, *Chalcoëla* (= *Dicymolomia*) *pegasalis* Walk., which is absent from the islands where the wasp is abundant.

The complex of forms included by Bequaert (1943c) under the name *Polistes canadensis* (L.) will probably ultimately be recognised as consisting of a number of species. Varieties likely to resemble the British Guiana forms in their biology have been observed by Rau (1933: 97, figs. 46-53) and FitzGerald (1938: pl. 1, fig. 1; 1939). Rau found many nests on Barro Colorado Is., some of them with as many as 1000 cells. He found clear evidence for the foundation of nests by swarming, and probably for the presence of more than one egg-laying queen. As parasites or scavengers in the combs he found the Phorid fly, *Megaselia* [*Aphiochaeta*] *scalaris* (Loew), and two moths, *Antispila* sp. and PHYCITINAE sp. FitzGerald states that the species is common in all the settled areas of Trinidad, and he records the association with it of ants and certain birds (cf. p. 99). As parasites or scavengers in the combs he found an undetermined mite, and the moths, *Tinea latebricola* Meyr., and *Epitheatia sphecephila* Meyr. FitzGerald considers that *Mischocyttarus labiatus* (Fab.), *Eumenes canaliculata* (Oliv.) and *Batazonus fervidus* (Sauss.) are homoiochromic with *P. canadensis*.

10. *Polistes crinitus* (Felton, 1764).

This species does not occur in British Guiana. Specimens recorded by Bodkin (1917), were, judging by those in the British Guiana Dept. Agric. collection, either *P. versicolor* (Oliv.) or *P. ruficornis* Sauss. var. *demeraraensis* Beq. As, however, we made some observations on the var. *multicolor* (Olivier, 1791) in Dominica, and on the var. *insulicola*, described by Bequaert and Salt (1931: 793) from St. Kitts, the species is included here. We found more than four nests on the island of Dominica and three on St. Kitts.

Nest 360, Dominica, Roseau Valley, beneath fern on bank, 3 ft. from ground, 9.x. There were 48 cells, with 6 empty, 22 eggs, 12 larvae and 8 pupae. the cells nearest the petiole contained eggs and were being used for a second time. The cells furthest from the petiole also contained eggs or very young larvae and were evidently the most recently constructed. There were 5 wasps; 1 queen, with 17 ovarial eggs, 1 intermediate, and 3 workers with filamentous ovaries. Six more workers emerged between 9 and 26.x.

Nest 362, same locality, on rock, 9.x. There were 82 cells, 3 empty, 34 eggs, 24 larvae and 21 cocoons. Five wasps were present but they were not dissected; 17 more emerged before 26.x.

Nest 363, same locality, beneath eaves of a hut, 8 ft. from ground, 9.x. There were 118 cells, with 51 eggs, 35 larvae, and 32 cocoons. The part of the comb near the petiole contained cocoons, except for a few cells being used a second time and containing eggs. Ten wasps were taken with the nest, but this was only about half of those present. The others were sitting on the eaves, facing outwards from the nest, within 5.0 cm. of the petiole. The 10 wasps dissected consisted of 1 queen (30 ovarial eggs), 7 workers and 2 intermediates with slightly more developed ovaries.

Another nest on the eaves nearby consisted of about 20 shallow cells, apparently containing eggs, and 15 wasps either on or near it, sitting on the eaves with their heads outwards from the petiole. Such a nest must have been recently founded by a swarm. The eaves nearby had numerous nests of all sizes.

Nests 372-4, St. Kitts, Old Road River, 28.viii., two on a small tree and one on an overhanging rock. They had 17, 27 and 62 cells, and 2, 5 and 18 wasps respectively. The eggs and young larvae were attached by a short stalk from the hinder end, half-way up the sides of the cells. The wasps were not dissected.

The Dominica nests were pale grey and fibrous. The cells were 4.0×15.0 mm. The cocoon-caps were domed, rising 2.0-4.0 mm. above the distal end of the cells, often projecting more on one side than the other. The St. Kitts nests were brown, and the cocoons were domed but not really projecting. The wing-lengths and hamuli numbers of 3 queens, 6 intermediates and 11 workers were: 11.5-13.5, mean 12.5, 10.5-13.0, mean 11.7, 10.0-13.0, mean 11.3 mm.; 17-20, mean 18.0, 14-18, mean 16.3, 14-19, mean 16.6, respectively. Workers and intermediates do not differ significantly; the queens probably show a real difference, but the numbers are too small to test. According to Ballou (1915, 1934), *P. crinitus* is abundant in many of the Leeward Is., especially where *P. canadensis* var. *cinctus* Lep. is absent. As in that species, its numbers are much affected by the Pyralid, *Chalcoëla pegasalis* (Walk.).

12. WASPS, ANTS AND BIRDS.

Ants may act either as enemies or as protectors of social wasp colonies. The former relationship is probably much the commoner, but both may have had a considerable influence on the evolution of social life. There are no proper statistics for the abundance of ants in the various major regions, but it is evident from the number of species and from casual observation of the number of individuals and of colonies that they are a major factor in the tropical regions where the social VESPIDAE (except possibly the VESPINAE) evolved.

Probably many wasps' nests are destroyed by the small-scale predatory activities of the MYRMICINAE and PONERINAE, but a more spectacular destruction is caused by the DORYLINAE (Driver Ants). In this subfamily, according to Emery (1910) and Wheeler (1913), most species fall into two large genera. *Dorylus*, mostly found in Africa but extending into Indo-Malaya; and *Eciton*, with even more species, found between the southern United States and Argentina. The distribution of Driver Ants, indeed, very nearly corresponds with that of pleometrotic wasp colonies.

Most Driver Ants appear to make no permanent nests, but have temporary homes from which bands of workers issue forth, usually at night, to raid the surrounding country. All forms of insect life seem to be killed and carried back, but wasps' nests, with their rich store of helpless larvae, might well be a specially attractive source of food. Fiebrig (1917) has described the raids of *Eciton vagans* Oliv. on *Polistes* nests in Paraguay. They were made at night, when all the wasps were at home, but perhaps somewhat lethargic from the cold. Many of the adult wasps were killed but the early stages (including eggs and pupae) were taken back alive to the temporary ants' nest.

Fiebrig estimated that one colony of *E. vagans* was destroying 2-4000 wasp larvae a night. Other records of such attacks are the following: Wheeler (1925) records *Eciton hamatum* Fab. attacking a nest of *Polybia* sp. in Panama; Schwarz (1931)—*Eciton* sp. attacking *Polybia occidentalis* (Oliv.) in Panama; FitzGerald (1938: 182)—*Eciton burchelli* Auct. attacking *Polistes canadensis* (L.); Myers (1929: 87) gives two references to Driver Ants attacking wasps and one to an occasion where they seemed to be ignoring *Polistes* nests; attacks of *Eciton* on *Polybia occidentalis* (Oliv.) and *Parachartergus fraternus* (Grib.) are described in the present paper. It is not yet possible to assess the frequency of such attacks, but one has the impression, in the Guiana rain forest, that any nest which lasted for more than a few months would run the risk of attack.

There appear to be four ways in which destruction by ants could be more or less avoided: (a) Wasps might nest in habitats which are largely avoided by Driver Ants. Our impression in British Guiana was that the Ecitonini tend to inhabit the taller forest, are less frequent in second-growth forest and are almost absent from clearings. It is possible that the larger and more permanent wasps' nests tend to be built in such situations (e.g. *Polistes*). Much more evidence, however, is required, since wasps' nests are much harder to find in tall forest, particularly at any height above the ground. Possibly the large trees on the edge of rivers, which are inhabited by such species as *Chartergus chartarius* (Oliv.) are partly protected by floods.

(b) Wasps might make numerous small, somewhat ephemeral nests. This appears to be the solution adopted by numerous species, but many of the apparent examples need careful consideration. In general (p. 124), it is more efficient to run a colony for as long as possible; a short-lived colony would perhaps only be advantageous if ant attacks were very severe. On the other hand, in many species (e.g. *Mischocyttarus* p. 116, *Polybia occidentalis* (Oliv.)) larger colonies are produced in the subtropics than near the equator, though there is no evidence that the frequency of ant attacks varies in the same way. It would seem that the small equatorial colonies are at least partly the result of climatic conditions.

(c) Wasps might develop the form of social life which would suffer least from ant attack. This is what most POLYBIINAE seem to have done. The egg-laying queens, which are often numerous, retain their mobility. When the nest is attacked the adults may fly off, sacrificing the brood, as described under *Parachartergus fraternus* (Grib.). The pleometrotic colony not only preserves its mobility but has the power of rapidly producing a new lot of eggs.

(d) The wasp colony may seek protection from some species of ant.

Ant colonies which often persist for many years are as exposed to the attacks of Driver Ants as are those of wasps. Several ants of the subfamily DOLICHODERINAE (*Azteca* spp., *Dolichoderus* spp.) have enormous colonies inhabiting carton nests, the sections of which cover the greater part of whole trees. How these colonies protect themselves is not known; they are certainly very active in attacking any vertebrate climbing on their tree. Any insect which can find a *modus vivendi* with the DOLICHODERINAE, or with the other tree-inhabiting ants, will obtain at least a measure of protection from the Driver and other predatory ants, as well as from vertebrates. It is convenient to

mention at the same time the records of birds nesting on "ant-trees," since, in many cases, all three groups of animals are found together. The principle data will be found in the following papers: Wasps and ants (and birds)—Ducke (1906: 18-19; 1910: 457-8; 1914: 323), FitzGerald (1938: 186), Myers (1929; 1935), Richards (1945: 305); Wasps and birds only—Alexander (1931), FitzGerald (1938: 182), McAtee (1929), Myers (1929; 1935; 1935a). Most of the earlier records which were collected by Myers are not cited separately. Myers (1929, 1935) has given an admirable discussion of the subject, principally from the point of view of the birds.

Certain birds seem to choose as nesting-sites trees on which ants or ants and wasps are already nesting. There is no evidence that the birds provide any protection to the insects. The chief birds with this nesting habit in Guiana are Orioles of the genus *Cassicus*. Where ants are not present, the wasps are usually species of *Polistes* (in S. America, especially *P. canadensis* (L.)).

The relation of the wasps to the ants seems to be similar to that of birds, except that there is likely to be an element of mutual protection. The ants are usually Dolichoderines, and most of the evidence suggests that they build in the tree first. The wasps that are most often recorded as entering into such associations are *Polybia rejecta* (Fab.) (very often; see also p. 40), *P. lugubris* Sauss., *Stelopolybia pallipes* (Oliv.) var. *myrmecophila* (Ducke), *Synoecca surinama* (L.), *S. virginea* (Fab.) (= *irina* Spin.) (Ducke, 1905a; 1905; 1907), *Protopolybia emortualis* (Sauss.) (see p. 22), and certain species of *Mischocyttarus*. There is little doubt that the ants do give some protection to the nests of those wasps able to establish relations with them, but whether this happens often enough (apart, perhaps, from *Polybia rejecta*) to be a factor of importance in evolution is still uncertain.

Little is recorded of birds as enemies of S. American wasps. FitzGerald (1938: 185) found *Mischocyttarus surinamensis* (Sauss.) in the stomach of a swift, and Bertoni states that a woodpecker (p. 53) is a serious enemy of wasps' nests in Paraguay; he even suggests that the spiny envelope of nests of *Polybia occidentalis* var. *scutellaris* (White) is a protection against this bird.

13. THE STREPSIPTEROUS PARASITES OF POLYBIINAE.

Previous records of stylopised POLYBIINAE are not very numerous and appear to be based entirely on puparia, except for the record of Brèthes (1923). Ducke, it is true (1910: 457), speaks of stylopised *Mischocyttarus* as common, but they have not been described or bred out. Richards (1945: 304-5) found only two stylopised specimens in 1335 wasps of the genus examined; the published records concerned four species. Salt and Bequaert (1929) record 20 stylopised specimens of nine species of *Belonogaster* from Africa. In the other genera of POLYBIINAE the following seems to be a complete list of records, including published observations, material found in the collection of the British Museum, and specimens collected by us in British Guiana. The notation used is that of Salt and Bequaert.

1. *Brachygastra lecheguana* (Latr.) (as *Nectarina*). PERU: R. Putamayo, Tacna, 28.viii.1920, female with ♀—5 R (Salt and Bequaert, 1929: 261).
2. *Protopolybia minutissima* (Spin.). In nest 211 (p. 20), 3 workers

were found with 1 larva and 2 very immature males, respectively in their abdomens. The males are XENIDAE, of a genus at least very close to that attacking *Polybia rejecta* (Fab.) (see below). The proportion of infected wasps in the colony was 0.4 per cent.

3. "*Polybia nigra* Sauss." Amazons, R. Juruá, 7.v.1903, one worker with ♀—4 (R. von Ihering, 1904: 254). According to Ducke (1910: 503), the specific identity of the wasp is doubtful.

4. *Polybia sericea* (Oliv.). BRAZIL, one female with ♀—4 (Smith, 1859: 131). The specimen has not been found in the British Museum collection.

5. *Polybia occidentalis* (Oliv.) var. *scutellaris* (White). BRAZIL, female (R. von Ihering, 1904: 296).

6. *Polybia occidentalis* (Oliv.) var. *albopicta* Smith. BRAZIL, female with ♀—4 R (Swainson), in coll., B.M.

7. *Polybia occidentalis* ssp. *platycephala* Rich. Nest 26 (p. 44), two workers with late Strepsipterous larvae in the abdomen. Nest 339 (p. 46), two workers with early Strepsipterous pupae in the abdomen.

8. *Polybia occidentalis* ssp. *spilonota* Cam. NICARAGUA: Managua, male with ♂—5 centre (Baker), in coll. B.M.

9. *Polybia parvala* (Fab.). Nest 85 (p. 54), one worker with a ♂ puparium.

10. *Polybia rejecta* (Fab.). Trinidad, i-ii.1931, female with ♀—4 R (A. K. Totton), in coll. B.M.

Nest 309 (p. 42), four workers (0.2 per cent.), three with ♂, one with ♀ Strepsipteron: 1 ♂, 1 ♀ were very immature, but 2 ♂ were fully developed and ready to emerge. They belong to the XENIDAE, but will not run to any of Pierce's subfamilies (1909: 71), for they have two maxillary palp segments, the metathoracic scutellum is pedunculate, but the postlumbium is about as long as broad. They seem to belong to an undescribed genus.

11. *Polybia rejecta* (Fab.) var. *litoralis* Zav. BRAZIL, male with ♀—4 R (F. Smith coll.), in coll. B.M.

12. *Stelopolybia pallipes* (Oliv.) var. *bequaerti* Rich. BRAZIL, male with ♀—4 R (F. Smith coll.), in coll. B.M. BRITISH GUIANA (p. 75), male with ♀—5.

13. *Parachartergus fraternus* (Grib.). BRAZIL: Itacoatiara, viii.1935, female with 2 ♂—5 (G. V. Vredenburg), in coll. B.M. The specimen shows no modification and very little distortion.

As is usual in wasps with progressive provisioning, none of the styloped specimens shows any serious external changes.

14. THE RATE OF CELL-CONSTRUCTION AND THE RATE OF OVIPOSITION.

Some social insects, such as ants, make piles of eggs in certain nest-chambers, so that space alone is never likely to be a reason for limiting the number of eggs. In *Bombus* the eggs are laid in waxen pockets attached to the outside of the groups of cocoons. According to Brian (1948), the number of eggs in a pocket is related to the number of cocoons in the group to which it is attached. In the VESPIDAE, on the other hand, each egg is laid in a separate cell, and it is difficult to determine whether the oviposition rate is controlled by the rate of construction or vice versa.

Examining 56 nests of 12 species for which data are available, it is found that there is a wide variation in the number of empty cells; on the average,

about one-fifth (19 per cent.) are empty. If only the short-cycle species are considered (47 nests of 9 species), it is found that after a short initial period, when most cells are occupied, about 40 per cent. of the cells are empty, on the average. This suggests that the oviposition rate may be the limiting factor, but it is possible that there is a definite policy of keeping construction ahead of oviposition.

More cogent evidence can be obtained by studying the rate of construction in relation to the number of queens and the number of workers (33 nests of 8 short-cycle species). Dividing the estimated age of the nest into the total number of cells gives a figure for the number of cells constructed per developmental period, and this can be related to the numbers of queens and workers as follows:

	No. of queens		
	1-6	9-28	48-176
Mean no. of workers*	58	140	348
Mean no. of cells built per developmental period	637	841	2650

* Intermediates are included with workers.

The rate of cell construction appears to be related both to the number of queens and to the number of workers. But the latter number itself depends on the past rate of construction, and probably also on the number of queens. The problem therefore is best analysed by calculating the correlation coefficients between the rate of cell construction ($=y$), the number of queens ($=x$) and the number of workers ($=z$), the records for 33 nests being given in Table 24. The following values were found: $r_{xy} = +.7345$; $r_{xz} = +.4685$; $r_{yz} = +.5192$. For 31 degrees of freedom all these coefficients are significant ($P < .01$). If, however, the three partial correlation coefficients are calculated, $r_{xy.z} = +.6506$ ($P < .01$), whereas the other two partial coefficients, though positive, are well below the level of significance. It would appear, therefore, that the number of queens (which must largely determine the potential oviposition rate) controls the rate of cell construction.

It is therefore legitimate to calculate the regression of cells per worker per developmental period ($=r_1$) on the number of queens ($=x$), in the same 33 nests. The mean value of r_1 is 13.99 and its regression on x takes the form $r_1 = 13.99 + .25(x - 22.48)$. The regression coefficient is significant ($P < .01$). This may be reduced to the form of the final section of this paper by converting to days (assuming a developmental period of 21 days). The equation then takes the form $r = .0119q + .3986$, where q is the number of queens, and r the number of cells constructed per worker per day.

Evidently a balance must be kept between the number of workers and the number of queens. Founding swarms must have approximately the right proportions of the two castes, and in small, short-lived colonies few queens can be produced or else each one cannot be accompanied by a sufficient number of workers. In long-lived colonies the difficulty would rather be to prevent the proportion of workers to queens from becoming too high. Possibly such colonies reach a balance between the production of new workers and the death of old ones. Another alternative would be for young queens to be received back

into the nest after fertilisation. This appears to happen in some ants; there is no evidence for it in the POLYBIINAE, but it would be very difficult to detect.¹⁸ It might, perhaps, especially be expected in the very large, long-lived colonies which are found in the subtropics.

TABLE 24.

Number of queens ($= x$), number of workers ($= z$), cells per developmental period ($= y$), and cells per worker per developmental period ($= r_1$) in 33 colonies of short-cycle POLYBIINAE.

x	z	y	r_1
1	23	448	20.35
1	32	770	24.06
1	24	361	15.04
1	36	207	5.75
1	55	258	4.69
1	5	173	34.60
1	21	129	6.14
1	156	189	1.21
3	48	734	15.29
4	51	3230	63.33
4	116	197	1.70
4	13	268	20.62
4	156	2636	16.86
5	36	135	3.75
6	91	251	2.76
6	67	210	3.13
9	206	743	3.61
10	98	815	8.32
10	75	125	1.67
11	148	1056	7.27
11	78	557	7.14
11	14	259	18.50
12	42	352	8.38
19	144	605	4.20
21	603	2672	4.43
23	82	580	7.07
26	73	2348	32.16
28	114	583	5.11
48	548	1339	2.44
56	119	296	2.49
90	300	475	1.25
137	721	5740	7.96
176	50	5400	108.00
Means 22.48	131.67	1034.40	13.99

The numbers of workers recorded make no allowance for any deaths that there may have been during the life of the colony. Regression equations (P in all cases $< .01$).

$$y = 1034.40 + 26.32 (x - 22.48).$$

$$z = 131.67 + 2.02 (x - 22.48).$$

$$y = 1034.40 + 4.31 (z - 131.67).$$

¹⁸ As pointed out on p. 80, our small body of data for *Stelopolybia pallens* (Fab.) would be consistent with this hypothesis.

There are no direct observations on the oviposition rate of female POLYBIINAE, but there are three quantities which are probably correlated with it.

1. Eggs/queens. Dividing the number of queens in the colony into the number of eggs in the cells, shows the average number of eggs which each queen must have laid in a preceding period equal to that of incubation under the prevailing conditions. (Symbol— y .)

2. The number of ovarial eggs per queen. This number tends to increase as the queen ages, and to be inversely related to the number of queens. (Symbol— w .)

3. The ratio eggs/ovarial eggs, which is the number of eggs in the comb divided by the total number of ovarial eggs in all the queens. This relates the state of ovarial development to recent oviposition, and is perhaps the best measure of the demands on the female, since it relates the eggs to the actual, rather than the potential, source of supply. (Symbol— t .)

These three variables can be correlated with the age of the colony ($= x$) and the number of queens ($= z$). The data from 39 nests of 9 short-cycle species have been collected in Table 25, below.

The irregularities of the figures in Table 25 are probably partly due to the approximate nature of the estimates of age of nest and of number of eggs in the cells, and perhaps also to treating together a number of species. Nevertheless, the intricate correlations which can be shown to exist between the variables are at first difficult to realise, and a big allowance must be made for the range in the number of queens.

Dealing first with the age of the colony (x), the ratio eggs/queens (y) and the number of queens (z), the partial correlation coefficients are: $r_{xy-z} = +.5730$, $P < .01$; $r_{yz-x} = -.3312$, $P < .05$; $r_{xz-y} = +.05$, not significant. Thus, there is a direct relation between age and the ratio eggs/queens when the effect of the number of queens is eliminated and the ratio tends to be smaller when queens are more numerous (the effect of age of colony being eliminated). That is, with more queens, each one lays less, and the accumulation of eggs is smaller than would be expected from the performance of a single queen. The oviposition rate tends to increase with the age of the colony; the figures give no clear sign of a falling off.

Bringing in now the variable, w , the mean number of ovarial eggs per female, the following partial correlation coefficients may be obtained: $r_{xy-w} = +.5422$, $P < .01$; $r_{xw-y} = -.14$, not significant; $r_{yw-z} = +.6153$, $P < .01$. Thus, the age of the colony is not significantly correlated with the number of ovarial eggs per female when the effect of ratio eggs/queens is eliminated, but the mean number of ovarial eggs is significantly correlated with the ratio eggs/queens (effect of age of colony eliminated). This probably means that the mean number of ovarial eggs is closely related to the oviposition rate.

Finally, the effect of the number of queens on the oviposition rate may be examined by calculating the partial correlations between z and w and t (ratio eggs in cells/total ovarial eggs). The following values are obtained: $r_{zw-tz} = -.5203$, $P < .01$; $r_{zt-wz} = -.3852$, $P < .02$.

Thus, it appears that whichever of the available measures of oviposition rate is used, the rate is reduced when more queens are present; there is less laying by each one, even though the accumulated total becomes greater. On the other hand, only y (eggs/queens) is significantly correlated with x

TABLE 25.

Data for analysing oviposition rate in short-cycle POLYBIINÆ (39 nests of 9 species). Colonies in which queens were not properly dissected or in which there were no eggs in the comb are excluded.

Age <i>x</i>	Eggs/♀ <i>y</i>	No. of ♀ <i>z</i>	Mean no. of ovarial eggs <i>w</i>	Eggs/ovarial eggs <i>t</i>
0.10	2.8	176	2.00	1.4
0.10	34.0	137	3.75	0.9
0.10	30.0	1	10.00	3.0
0.10	35.8	4	18.30	2.1
0.34	15.0	4	2.25	6.7
0.37	33.3	6	11.00	3.0
0.40	14.2	5	7.40	1.9
0.40	36.0	1	6.00	6.0
0.60	21.8	11	3.70	5.9
0.62	7.5	16	1.75	4.3
0.63	35.2	11	9.40	3.7
0.63	5.2	28	4.50	1.2
0.66	23.0	26	4.40	5.3
0.66	62.0	1	19.00	3.3
0.68	9.3	10	3.00	3.1
0.71	8.3	12	14.30	0.6
0.73	6.3	11	5.30	1.2
0.76	78.0	3	6.30	12.4
0.79	5.2	23	6.50	0.8
1.10	50.0	1	24.00	2.1
1.10	57.9	9	12.75	4.5
1.10	82.0	1	14.00	5.9
1.10	91.0	1	18.00	5.1
1.24	46.7	3	8.00	5.8
1.40	4.0	56	3.00	1.3
1.40	161.0	1	18.00	8.9
1.40	22.5	6	11.20	2.0
1.40	113.0	1	17.00	6.6
1.40	3.6	27	3.56	1.2
1.40	4.1	33	4.00	1.0
1.40	140.0	1	10.00	14.0
1.43	14.4	48	5.40	2.7
1.65	95.0	21	13.70	7.0
1.77	17.8	5	9.40	1.9
2.40	174.0	1	22.00	7.9
2.40	4.2	90	2.50	1.7
2.40	71.0	4	12.00	5.9
2.40	30.0	5	17.20	1.7
2.70	33.2	6	12.30	2.7

NOTE.—One nest, no. 26 of *P. occidentalis platycephala* (not included in the Table), was of rather doubtful age, apparently 0.0, while the mean ovarian egg number was as high as 27.0. It is probable that the colony had recently been founded by wasps whose first nest of age 1-2 had been destroyed.

(age of colony); none of the correlations or partial correlations between t and w and x was significant; it is probable that y is the best measure of the current oviposition rate, whereas w or t measure rather the accumulated total of eggs which has been laid by each female. It is also likely that a check to the oviposition rate will also lead, at any rate for a time, to a high number of ovarian eggs.

If the oviposition rate were constant, it would be expected that after one developmental period had elapsed the eggs, larvae and pupae would occur in proportion to the duration of each stage. The average proportions actually observed in 12 species were $4:3:3$, approximately. The durations are not known, but on p. 10 they have been assumed to be related as $2:4:4$; it is, at least, extremely improbable that the egg-stage can be the longest. No doubt part of the discrepancy is due to the very rough (p. 17) estimates of numbers that have had to be used. Nevertheless, using accurate data in *Bombus*, Cumber (1949: 35-6) found a similar discrepancy which he attributed to egg eating¹⁹ by the workers. Such behaviour is not known in POLYBIINAE, but might occur. A continuously rising oviposition rate, such as has been established in the previous paragraphs, might also produce an excess of eggs over the other stages.

However, in 45 nests of 9 short-cycle species, the age of nest was plotted against eggs as a percentage of total brood with the following result:

		Age					
		0-10	0-34-0-40	0-60-0-79	1-10-1-24	1-40-1-77	2-40-2-79
Mean	percen-						
tage	of eggs	100	45	44	47	42	43

There seems, therefore, no tendency for the excess in the number of eggs to alter with the age of the nest. The question must be left for future investigation.

As already noted, Brian (1948) has found in *Bombus agrorum* (Fab.) that the number of eggs laid is linearly related to the number of cocoons. As Brian points out, this will prevent the young brood from exceeding by too much the number of workers likely to be available for their care, and this might be important if there was much mortality in the early stages.

On the other hand, a real regulation of the growth of the colony would seem to require that the oviposition rate should be related to the size of the whole colony, not merely to the numbers of one stage. For, if the length of pupal stage exceeds that of the egg stage, the number of pupae available will tend continually to increase. It appears, indeed, from Cumber's (1949) data that the oviposition rate in *Bombus agrorum* does increase up to the time that queens are first produced and then falls suddenly. The relationship discovered by Brian may perhaps hold for most of the life of the colony, but not for the last part.

15. THE DIFFERENTIATION OF CASTES.

It has become apparent that the castes of the VESPIDAE present a more complicated problem than used to be supposed. Heldmann (1936) and Pardi

¹⁹ It was necessary to assume that eggs were eaten at night, whereas counts of eggs were mostly made in the afternoon.

(1942; 1946), for instance, have shown in *Polistes gallica* (L.) that, though several queens may found a colony together, one of them becomes the real queen, and the egg-laying function and ovaries of the others (the auxiliaries) become more or less suppressed. Probably the queen is the one whose ovaries happen at the start to be best developed and she so dominates and terrorises the others that they gradually cease egg-laying. The energy they have to expend on foraging and building, and the extra food which the dominant female receives from them, together accentuate the small original difference in the ovaries. Again, Pardi (1943) and Deleurance (1946) have shown in *Polistes*, and the same is probably true of all haplomictic colonies, that when the queen dies at a later stage in the life of the colony, some of the workers may develop their ovaries and lay eggs, though these produce only males. As this oviposition may start within 24 hours of the removal of the queen, her suppression of worker oviposition must be largely direct.

It is proposed now to list all the factors which may possibly contribute to the production of different types of female. No doubt there may be some as yet unthought of, and in different genera, or even in one species, several of them may play some part.

1. *Differential larval feeding.* There is so far very little direct evidence for this, and Pardi could not detect it in *Polistes*, though the structural differences which we have found between queens and workers in some POLYBIINAE can scarcely have any other explanation. Besides the supply of different quantities or qualities of foods, which (see below) might be a cyclical phenomenon, there might be distribution of some secretion (which might also be cyclically produced). The effect of a secretion²⁰ could be either positive or negative. Differential feeding could also result, as it does in *Bombus* (Cumber, 1949), if the position of the larva in the comb influenced the amount of food received.

2. *Trophallaxis.* It is well known that worker wasps largely partake of the salivary secretion of the larva they look after, receiving it in exchange for food brought into the nest. Mr. G. E. J. Nixon has told us how, under bad weather conditions which prevent foraging, the demands of the workers over two or three days may lead to a visible shrinking in the larvae. It is conceivable that variations in the trophallactic balance might contribute to the polymorphism of the adults.

3. *Differential feeding of adults.* Cumber (1949) has shown in *Bombus* that an essential difference between a large worker and a young queen is that the latter can feed up on honey and develop a large, fat body, whereas a worker cannot. On the other hand, Marchal (1897) has suggested a process of "nutritional castration," the nursing instinct of workers leading, by way of overwork and underfeeding, to ovarian suppression. Present evidence suggests that both these processes occur, but only to develop an already existing potential polymorphism. Thus, young queens which hibernate, and probably also the young queens of non-hibernating Polybiines, require at least more food than the workers. Nutritional castration, so far as it occurs, is probably a secondary consequence of dominance.

²⁰ Castle (1934), in *Zootermopsis* (Isoptera), gives good grounds for believing that all nymphs are potentially able to develop into males or females, but that their gonads are suppressed by a secretion produced by the sexual forms and handed about in the mutual exchanges of food.

4. *Dominance of the queen* (and to less extent of other individuals). This has already been discussed and is clearly important in all species as a factor in the suppression of ovarian development. In *Polistes* it may lead to the development of a special type of female, the auxiliary, but this cannot happen in strictly haplometrotic species (e.g. VESPINAE) or regularly pleometrotic colonies (e.g. most POLYBIINAE). The converse of the process is that on the death or loss of the queen, a new type of female, the egg-laying worker is developed.

5. Flanders (1942; 1945; 1946) has suggested that, as in some parasitic Hymenoptera, the nature of the adult may be affected by the time the parent egg spends in the female oviduct before being laid, through a process of differential absorption. His theory, apparently, demands that worker-producing eggs should be laid at a slow rate (i.e. maximum öosorption) and queen-producing eggs at a higher rate with no öosorption. The evidence at present suggests that the oviposition rate does rise continuously during the life of short-cycle colonies. The subject is clearly one which would repay detailed study.

6. *Cyclical factors*. This term may be applied to any aspect of behaviour or physiology which is a necessary result of the age of the colony or of the individual. The simplest factor of this sort is a change in the larva/worker ratio. This is considered theoretically later (p. 121), and in the succeeding paragraphs it is examined in a number of POLYBIINAE. There could, also, be a cyclical development of some secretion, as there is in the workers of *Apis*. A cyclical factor which is certainly of some importance is the age of the queen. Because her life is relatively short, the possible duration of most colonies is limited, and this is likely to affect at least the later part of the life of the colony, if only by changes in the oviposition rate. Deleurance (1948; 1948a) has recently strongly supported the view that the whole nest-cycle of *Polistes* is due to an intrinsic cycle in the development of the queen. He finds that in a constant temperature room, with uniform feeding, colonies produce sexual forms after a fixed lapse of time, irrespective of the size of the comb and sometimes before any workers have emerged from their cocoons. This subject also appears in need of much more study. Both Weyer (1927; ants) and Pardi (1946; *Polistes*) have recorded the partial and temporary development of the worker ovary at a certain age, or at certain times of the year.

Before turning to the detailed facts concerning the POLYBIINAE, it will be useful to examine Table 26, in which are shown the six types of female²¹ which have been found in various wasps' nests. The classification proposed is tentative and unlikely to be final.

Our S. American material can be classified as follows. In the POLISTINAE, 7 nests of 3 species were investigated. In all of them there was only one queen, and intermediates were found in all but one (*P. carnifex* F.). The intermediates in *P. canadensis* were more like queens, in *P. crinitus* more like workers.

²¹ In VESPIDAE (as in *Bombus*) queens before hibernation never show any sign of ovarian development, and this is in fact a distinction between them and workers in the late summer. Queens of tropical species which do not hibernate, probably feed up in the parent nest and may well show signs of ovarian development before fertilisation. For this reason, it is often impossible to know how to assess intermediates found in colonies which have reached the reproductive stage.

TABLE 26.

Possible types of females in the social VESPIDAE, based chiefly on personal observations and on the work of Pardi (1940-47).

Description of caste	Character	Conditions for presence	Example
Egg-laying queen	Sperm present ; ovaries developed	Necessary for founding colonies ; sometimes lost later	All spp.
Auxiliaries	Sperm present ; ovaries degenerating	Foundation of colony by more than one queen in haplo-metrotic species. Disappear on the appearance of first workers	<i>Polistes gallica</i> (L.)
Young queen	Sperm not necessarily present ; ovaries undeveloped. Only recognisable if castes externally distinguishable	Attainment by colony of reproductive stage usually shortly before its end, but cyclically in long-lived Polybiine colonies	All spp.
Intermediates (? = females of transition of Pardi, 1946)	Sperm not present ; ovaries partially developed	Not known ; possibly derived from larvae which have received insufficient of queen-producing treatment	Many POLYBIINAE, some <i>Polistes</i> .
Laying workers (= females of substitution of Pardi, 1946)	Sperm not present ; ovaries developed.	Chiefly developed when queen dies in haplo-metrotic colonies	<i>Polistes Vespa</i> (s.l.).
Sterile workers	Sperm absent ; ovaries undeveloped	Always present in pleo-metrotic colonies ; present after first brood hatches in haplo-metrotic species	All species, except social parasites.

A proper development of a classification of the females requires not only more dissections, but a study, especially in *Polistes*, of the minor structural characters separating queens and workers.

In the POLYBIINAE 64 nests of 7 genera and 15 species were investigated. From the present point of view the species can be divided into three types.

1. Number of queens variable, but often only one. Intermediates few and normally present only nests with one or few queens. *Polybia* (6 species), *Stelopolybia fulvo-fasciata*, *Parachartergus fraternus*, *Metapolybia cingulata*.

Summary of Group 1 (all species).

	No. of queens per nest						
	0	1	2-5	6-10	11-50	50-100	137
No. of nests	1	14	12	6	12	1	1
No. of nests with inter- mediates	0	9	1	0	2	0	0

Mean number of queens per nest, 12.0 (47 nests).

Number of nests with one or more intermediates, 12; mean number of queens in these nests, 3.6.

2. Nearly always many queens; many intermediates, often grading into queens. *Brachygastra scutellaris*, *Stelopolybia pallens* (one nest with as few as 4 queens), *Protopolybia pumila*, *P. minutissima* (two nests with only 2 and 3 queens, respectively); also, probably, *Belonogaster* in Africa. *Protopolybia holoxantha* and *P. emortualis* were not satisfactorily studied, but seem to belong to the same type.

Mean number of queens per nest (for the first four species) 47.5 (13 nests). Intermediates always present and often more abundant than queens; in ovarian development they tend to grade into the queens, especially in the smaller colonies. In *Stelopolybia pallens* queens can only be recognised by the presence of sperm in the receptaculum; the transition in ovarian development is complete and even the workers are hardly more than one end of a series. Nevertheless, in the three other species the queens differ significantly from the worker in skeletal structures, so that they must in some way receive different treatment as larvae. It is possible either that definite queens are reared or that certain individuals have happened to receive better treatment than their fellows (as Cumber (1949) has shown for variations amongst *Bombus* workers). In either case, the structural differentia of the queen must be attributed to larval history. There is no obvious reason in the habits of these species why they should differ in caste-differentiation from those of Group 1. We are inclined to think that they may represent a less specialised stage in social evolution. In structure *Brachygastra* is probably the Polybiine which most resembles a solitary wasp; *Protopolybia* is relatively primitive, but *Stelopolybia* and *Belonogaster* are relatively specialised.²²

3. Usually one queen; no intermediates; colonies usually very small. *Mischocyttarus*.

The data for this genus have already been published (Richards, 1945). The wasps from 6 nests of two species were dissected. In each of the 4 nests of *M. superus* Rich. there was one queen, but in the two nests of *M. lecointei* (Ducke) there appeared to be two, though the presence of sperm was not verified. There were no intermediates and the workers may possibly have differed from the queen in skeletal structures though the data were insufficient to prove this. The colonies studied were relatively large ones and it is certain that in most nests, at least in Guiana, only one queen is present. The ovary of the queen contains relatively few eggs. Nine queens of three species were dissected; they had 2-6, average 4.7 eggs, in their ovaries.

In large Polybiine colonies queens which have been laying for some time

²² This point cannot be fully elaborated until a study of the Vespid genera is complete.

can sometimes be picked out by the naked eye because the abdomen is swollen and paler. This has already been noted by Ducke (1910 : 461), but is only likely to be easy in nests with many queens. Not much has been recorded by earlier workers as to the numbers of queens or their difference from workers. The following is a summary.

Polybia occidentalis (Oliv.) var. *scutellaris* (White). No external difference except that the queen is perhaps a little larger, with brown, shining wings (H. von Ihering, 1896, 1896a ; R. von Ihering, 1903).

P. dimidiata (Fab.). Queen smaller (R. von Ihering, 1903).

Stelopolybia vicina (Sauss.). Queen larger, more robust, though of same length. Thorax and abdomen broader (especially the latter). Abdominal petiole very different ; shorter, depressed, twice as wide at base, where there is a small keel formed between two lateral depressions, campanulate before the mid-point, where it is twice as wide as proximally. Clypeus less shining and, like the abdomen, somewhat sericeous (R. von Ihering, 1903, 1904).

Both the von Iherings refer to the smaller receptaculum seminis of the worker, but we never saw any evidence of this. We detected no external difference between queens and workers in the following species : *Polybia bicyttarella* Rich., *P. catillifex* Moeb., *Stelopolybia pallens* (Lep.), *S. fulvo-fasciata* (Deg.), *Parachartergus fraternus* (Grib.) and *Metapolybia cingulata* (Fab.).

Significant differences²³ were as follows :

Polybia bistriata (Fab.). Queen with more hamuli than the worker intermediates nearer to the queen.

P. occidentalis (Oliv.) subsp. *platycephala* Rich. Queen with longer mesonotum, longer and wider 1st abdominal tergite, and with fewer hamuli per millimetre wing-length. Intermediates were rare and possibly were really young queens.

P. rejecta (Fab.). Queens with narrower vertex, shorter mesonotum, shorter proximal part but longer and wider distal part of 1st abdominal tergite.

Protopolybia pumila (Sauss.). Queen with longer wings and more hamuli than the worker. Intermediates resemble the worker.

P. minutissima (Spin.). Queens with wider 1st abdominal tergite than the worker, but queen, worker and intermediates all very similar.

Brachygastra scutellaris (Fab.). In one nest queens had more hamuli and less yellow on the scutellum than in the workers, but the differences in the other nest were not significant. Intermediates resembled workers.

Polybia occidentalis subsp. *occidentalis* (Oliv.) and *P. parvula* (Fab.) had slight but possibly significant differences between the queens and workers.

Polistes canadensis (L.) var. *cinctus* Lep. Queens with longer wings and more hamuli than the workers. The intermediates also differed significantly from the workers. They were smaller than the queens, but not significantly so. Similar differences were found in *P. crinitus* (Fulton) var. *multicolor* (Oliv.), but the numbers were too low to test significance.

Differences in hamuli-number may have a special significance. In a recent paper (Richards, 1949) evidence has been presented for the view that the

²³ It is important always to compare queens and workers from the same nest, or else proportionate numbers from different nests, as the wasps from different colonies are far from identical.

number is correlated with the distance likely to be flown in the life of the individual, an hypothesis still much in need of verification. It is only in social species that found colonies with swarms that the queen needs to fly less than the worker, and it is only in such Hymenoptera (MELIPONIDAE, *Apis*, *Polybia occidentalis platycephala*) that queens with fewer hamuli than the worker have been recorded. It should be noted that, as hamuli-number is strongly correlated with wing-length, a larger queen with longer wings would normally be expected to have more hamuli. Any reduction in hamuli-number is therefore very significant.

It seems clear that queens tend to be better differentiated in species which form larger colonies (a fact which may be relevant to the discussion of the larva/worker ratio on p. 121). This comes out most clearly when allied forms are compared, as below.

A. Queens well differentiated			B. Queens not or little differentiated		
Species	Mean no. of cells per colony	Mean no. of cells per queen	Species	Mean no. of cells per colony	Mean no. of cells per queen
<i>Polybia rejecta</i> . . .	7-8000	1152.4	<i>P. catillifex</i> . . .	135	70.4
<i>P. occidentalis platy-</i> <i>cephala</i>	812	59.5	<i>P. bistriata</i> . . .	335	166.9
<i>Protopolybia pumila</i> .	21,600	232.3	<i>P. bicyttarella</i> . .	341	130.2
			<i>Protop. minutissima</i>	1467	105.1

Within the species *P. occidentalis*, however, no relation was perceptible between size of colony and the degree of differentiation of the queens.

Perhaps the most significant character in the queens is the broader first abdominal segment which occurs in several species and may be related in some way to the potential development of the ovaries. As shown in the previous section, colonies with many queens develop more rapidly, but the ovaries of the queens and the oviposition rate are both smaller when the queens are numerous. The ratio cells/queens, which might be expected to indicate the the oviposition required of each queen, does not, however, seem to be closely related to the degree of caste-differentiation. The largest colony with a single queen was nest 146 of *Polybia bistriata*, with 461 cells. Weyrauch (1939 : 174) has recorded nests of *Polistes gallica* (L.), probably with single queens, with 500-580 cells (Sardinia).

What treatment is required to develop a larva into a queen is still quite unknown. In the VESPINAE, the queens are produced in special large cells which make up the last few combs to be built (occasionally there is a transitional comb with cells of two sizes). Males are produced at the time of transition, from either small or large cells (cf. Duncan, 1939 : 168). This is the only group of VESPIDAE in which the castes are sharply differentiated. Doubtless the large queen larvae are given more food than the smaller worker larvae, but no study has been made of this or of the conditions which would make more food available. The factors which may contribute to polymorphism in these social genera have been listed, but no more can be done at present, except to examine the changes in the larva/worker ratio in the Polybine colonies. It is suggested later (p. 121) on theoretical grounds that this ratio should decrease as the colony grows, so that each larva might expect more

attention. In forms with a low degree of caste-differentiation this might be the only mechanism required, though at the moment this can only be regarded as a possibility.

In Table 27 the data for the cell/wasp and larva/worker + intermediate ratios for all species are tabulated against the estimated ages of the nests. It will be seen that both ratios tend at first to increase with the age of the nest, then to diminish again, with some tendency to rise again at the end. The history of a typical short-lived colony²⁴ might be divided into three stages.

TABLE 27

All species of POLYBIINAE; age *vs.* cell/wasp and larva/worker ratios.

Stage of colony	Age of nest		No. of nests	Cells/wasps		Larvae/♀ + intermediates	
	Range	Mean		Range	Mean	Range	Mean
No. eggs hatched	0-0.10	0.08	6	0.7- 5.9	2.53	0	0
Initial colony	0.17-0.25	0.22	7	3.7-11.5	5.87	0.3-6.6	2.97
	0.29-0.39	0.34	7	2.6-13.3	7.51	1.1-6.8	2.86
Growth of larval nos.	0.40-0.51	0.43	4	3.0- 9.7	6.18	1.4-4.9	3.18
	1.10-1.27	1.18	5	3.8- 8.6	6.80	0.4-4.7	3.14
Production of males and queens	1.30-1.39	1.34	9	2.4- 7.0	4.54	0.7-3.6	1.96
	1.40-1.56	1.47	4	1.1- 5.8	3.35	1.1-2.4	1.70
Swarming	2.30-2.38	2.35	5	2.9- 6.8	4.34	1.1-3.0	2.16
	2+		3	3.1- 5.8	4.37	0-1.1	0.37

(1) The initial colony, up to about age 0.39. The ratio cells/wasps increases rapidly to a maximum, while the larva/worker ratio rises as the eggs hatch. (2) Ages 0.40-1.56. Relative growth of the adult population, leading ultimately to the production of males and queens. The cell/wasp ratio tends to fall but the figures are irregular, since in many colonies one or more new combs are added in the early part of the period. The larva/worker ratio goes down in a more regular way and this may be the cause of queen production at the end of the period, attention being diverted from nest building to care of the young. It is not known whether workers are still produced at the end of the cycle (they are not in *Vespula*) nor whether males are produced from eggs laid before the queen-producing eggs. (3) At the end of the colony, the cell/wasp ratio rises a little and the larva/wasp ratio may rise or fall. This suggests that swarms are leaving the nest and that finally no more larvae are being produced.

The initial great increase in cell number, followed by a check during which more attention may be paid to the larvae, might be compared to the two stages in the development of *Polistes* nests noted by Deleurance (1947). He finds that there is a period in which cell number increases, but the cells remain short, followed by one in which the number remains the same but the cells

²⁴ Long-lived colonies might go through an analogous cycle more than once.

are increased in length. During the second stage, males and queens are produced.

The larva/worker ratio could be reduced either by an *increase* in the number of workers or, after an interval, by a *decrease* in the oviposition rate, or by both together. The relation of the age of the colony to various measures of the oviposition rate was examined in the previous section, but there is no evidence for a fall in the oviposition rate, at least before the very end of the life of the colony. The changes in the larva/worker ratio should therefore perhaps be ascribed only to the relative accumulation of workers.

It has been suggested that the intermediates are probably best regarded as the products of larvae which have had some, but not sufficient, of the treatment which in fuller measure produces queens—except perhaps in some nests where they accompany males, and may be unfertilised queens. The evidence for this view is as follows: (1) They tend to be intermediates in both skeletal structure and in ovarian development. (2) If they were young queens, or queens which had failed to secure fertilisation and were degenerating into workers, they should be identical with the queens in skeletal structure. (3) In Group 1 of the POLYBIINAE they tend to be commoner when queens are few. This may suggest that they did not receive quite enough of the necessary treatment. (4) The intermediates in Group 2 are much more numerous; presumably in this group the mechanism of queen production has not been fully perfected. (5) The better differentiation of queens in larger colonies may be due to the lower value of the larva/worker ratio which results (p. 124) from the growth of the colony.

16. THE PRODUCTIVITY OF WASP COLONIES.

The success of a colony or its productivity is measured by the queens per queen to which it gives rise. In *Vespa* (s.l.), where the queens are easily recognised even when unfertilised, and where the colony is always founded by one queen, this quantity is easily measured. In the POLYBIINAE, however, there are serious difficulties. Young unfertilised queens cannot be distinguished with certainty from workers, so that even if enough mature nests had been studied, the problem would still be difficult. Moreover, different colonies are founded by different numbers of queens and workers. Fortunately, there are relatively simple, indirect methods by which a useful estimate of productivity can be obtained in the few species for which sufficient data are available.

The essential argument is that, *on the average*, the *final* composition of the colonies of a species (♀/♂ ratio) must be the same as the *initial* composition. Otherwise, the colonies would alter continually in one direction. While there is much variation from nest to nest, for each species the composition fluctuates about a mean.

The initial composition of colonies can be determined by considering nests of age less than one, in which no new workers have emerged. Queens can, in these, be separated from workers by the presence of sperm, and by the development of their ovaries. In Table 28 the data are averaged for all nests of age < 1.0 .

TABLE 28.

Composition of Polybiine colonies of age < 1.0.

Species	No. of nests	Mean age	Mean numbers of :			Percentage of :	
			Wasps	Queens	Workers + intermediates	Queens	Workers + intermediates
<i>Polybia bistriata</i> . . .	4	0.29	44.0	6.0	38.0	13.6	86.4
<i>P. bicyttarella</i> . . .	4	0.36	68.0	9.0	59.0	12.9	87.1
<i>P. occidentalis</i> (platycephala)	2	0.18	124.0	11.0	113.0	8.9	91.1
<i>P. parvula</i>	2	0.20	500.0	82.5	417.5	16.5	83.5
<i>P. catillifex</i>	2	0.22	11.5	2.5	9.0	22.0	78.0
<i>Stelopolybia pallens</i> . .	3	0.29	90.0	8.3	81.7	9.2	90.8
<i>Metopolybia cingulata</i> .	1	0.36	54.0	12.0	42.0	22.0	78.0
<i>Protopolybia minutissima</i>	2	0.34	75.0	14.5	60.5	19.3	80.7
All species	20	0.29	109.7	15.9	93.8	14.5	85.5

It will be seen that the average composition of these colonies does not vary so much as the crude data would suggest.

The final composition of colonies can be estimated by considering nests of age 2.0 +, in which males are present. This is possible for some of the species of Table 28 and for two additional ones. In interpreting these the following assumptions are made. It is assumed that the old queens do not take part in the formation of new colonies; even if they do so, this cannot contribute seriously to productivity in the present sense. The so-called workers in the mature colonies are taken to include the unfertilised queens, the number of which is determined by taking the same percentage of the total as queens are found to make up in the young colonies. In two species (*Polybia micans*, *Protopolybia pumila*) in which no young colonies were seen, it has been assumed that the sex ratio (δ /young queens) is the same as the average of all the other species. Thus, in these two species, also, a very rough measure of productivity is obtained. The data are collected in Table 29. It will, of course, be noticed that the number of nests available is really much too small; the regularities which appear are all the more significant. The figure of 38.0 for the productivity of *Polybia micans* is clearly much too high and it may confidently be predicted that the average number of founder queens is, in this species, nearer 10 than 1. The figure of 38 for the number of young queens may be approximately correct, since 28 "intermediates" were found by dissection to have ovaries rather well developed.

The figure 5.54 for the productivity of *Protopolybia* may also be too high. The nest with males was preserved in alcohol; sperm were not verified in the queens, which were identified by their ovarian development only. Consequently, some of the individuals classed as intermediates may have been less well-developed old queens; if only 9 of them were so, it would reduce the figure for productivity to 3.8.

While admitting that much evidence is still needed, we are inclined to think that the average productivity of a Polybiine queen lies between 1 and 4,

TABLE 23.

Composition of Polybiine colonies of age 2.0 +, with males present.

Species	No. of nests	Mean age	Mean numbers of				$\delta/100\phi^{\dagger}$	Productivity of	
			Wasps	Old queens	Males	Workers + intermediates		Queens	Colony ‡
<i>P. bistriata</i>	2	2.31	110.0	4.5	16.5	89.0	137.5	2.70	2.0
<i>P. bicinctarella</i>	2	2.38	113.5	5.0	17.0	91.5	144.0	2.40	1.3
<i>P. occidentalis</i> (s.s.)	1	2+	207.0	19.0	54.0	134.0	278.0	1.02	1.0
<i>P. micans</i>	1	2.38	197.0	1.0	40.0	156.0	105.0	[38]	
<i>Protopolybia pumila</i>	1	?	7087.0	93.0	213.0	7381.0	105.0	2.18	2.0
<i>P. minutissima</i>	1	2.31	693.0	21.0	69.0	603.0	59.0	5.54	8.0
<i>Metapolybia cingulata</i>	1	? 2.0	106.0	5.0	28.0	73.0	174.0	3.22	1.4

* The figure 8.9 per cent. (percentage of queens in young nests of *P. occidentalis platycephala*) is clearly too low, judging by the one nest available for *P. occidentalis occidentalis* so that the figure 14.5 per cent. (average for all the species) has been used.

† Sex ratio (excluding *P. micans* and *P. pumila*) = $188 \times 3/176.8 = 3.16 \delta/100 \phi$.

‡ The productivity of the colony is the number of new colonies which it might be possible to produce.

TABLE 30.

Estimates of the sex-ratio in *Mischocyttarus*, assuming queens and workers occur in equal numbers.

Estimate no.	Author	Material	No. of nests	No. of species	δ	All ϕ	ϕ	Queens	$\delta/100$ queens
1*	Zikán	All wasps examined			84	288	144.0	144.0	58.3
2	"	Wasps bred from cocoons	14	10	46	115	57.5	57.5	80.0
3	"	Nests containing some males	11	9	48	88	44.0	44.0	109.1
4	Richards	All wasps examined			276	1059	529.0	530.0	52.1
5	"	Nests containing some males	5	5	6	11	5.5	5.5	109.1

a very low figure compared with a non-social insect. To compare this figure with other families it would be required to know the length of the development period, so that the time taken for a queen to produce sexual forms could be calculated. From the observations, Schwarz (1931) on *P. occidentalis spilonota* (Cam.) (recorded as var. *scutellaris*), in Panama, the developmental period (egg to adult) is probably about 3 weeks. The total life of the short-lived colonies might then be about 9 weeks, and the figure for queens per queen per day would be something less than $\frac{4}{9} = .063$.

To compare with this figure, it is possible to get analogous estimates for *Mischocyttarus* and *Vespula*; there seem to be no adequate data for *Polistes*. In the first-named genus data have been obtained from the papers of Richards (1945) and Zikán (1935). The only record of the proportions of queens and workers is from our dissection of 18 wasps (9 ♀, 9 ♂) from four relatively old nests of two species. It may perhaps be taken that, in Guiana, the workers and queens occur in about equal numbers. There are a number of possible estimates of the sex ratio, as shown in Table 30. Estimates 1 and 4 are quite close, but, as Zikán has pointed out, it is probable that the males leave the nests fairly soon after they emerge, so that the figures may be unduly weighted in favour of the females, nearly all the wasps being caught on their nests. Moreover, many nests were taken at too early a stage to have produced any males. The estimates 2 and 5 for the ratios observed in nests containing at least some males happen to come at the same value and close to that for other Polybiines in Table 29, but the estimates from specimens actually bred from cocoons by Zikán is lower. It is possible that cocoons were not taken until some males had already emerged and left, but there is little doubt that the figure for ♂ : 100 ♀ in *Mischocyttarus* lies between 80 and 110. For estimating productivity, the data are assembled in Table 31.

TABLE 31.

Numbers of wasps on young and old nests of *Mischocyttarus*.

1. Richards, British Guiana; nests with no pupae yet present.
2. Zikán, Rio de Janeiro; nests with less than 20 cells (excluding a nest of *M. confirmatus* Zik. with 10 ♂).
3. Richards, British Guiana; nests with males present.
4. Zikán, Rio de Janeiro; nests with males present.

	No. of nests	No. of species	No. of females	Females per nest
1	35	9	48	1.37
2	6	5	15	2.50
3	5	5	11	2.20
4	9	7	88	9.78

It is probable that the excess over the figure of one female per nest in the young colonies is mostly due to workers accompanying the single nest-founding queen and less often due to the founding of nests by more than one queen. The maximum figures for productivity in British Guiana and Rio de Janeiro, assuming that every colony was founded by one queen, would be 2.20 and 9.78, respectively. Lower figures would be obtained if many of the females in the

old nests were workers; *i.e.* if half were workers, 1.10 and 4.89, respectively. All that can be said is that the figures are of the same order as in the other Polybiines.

The difference between the two geographical regions reflect the usual difference in the sizes of Polybiine nests in equatorial and subtropical regions, noted for most species. Taking nests of *Mischocyttarus* in which males were present, the average numbers of cells were: British Guiana 28.2 (5 nests of 5 species); Rio de Janeiro 83.5 (9 nests of 7 species).

Estimates of productivity in *Vespa* (*s.l.*) are much easier to make, since the colonies are founded by a single female, and young queens are separable from workers. Moreover, Weyrauch (1935) has collected from colonies in Western Germany a set of data which enables all the necessary calculations to be made, as shown in Table 32.

TABLE 32.

Productivity in *Vespula* calculated from Weyrauch (1935: Table 2) and, for the fourth column, from Weyrauch's Table 4. Only nests which contained males and young queens included.

Species	No. of nests	Total no. of combs	Cells per comb	Total no. of cells	Males	Females	Cells per young ♀	Productivity
<i>media</i>	3	11	132	1452	83	84	17.3	28.0
<i>sylvestris</i>	5	14	134	1876	157	161	12.4	30.2
<i>saxonia</i>	6	23	271	6233	211	171	36.5	28.5
<i>germanica</i>	13	100	807	80,700	4260	2180	37.0	167.7
<i>vulgaris</i>	4	28	753	21,084	550	150	(140.6)	(37.5)

The estimate of productivity is affected by the date at which the nest is examined. If too early (as in the nests of *V. vulgaris*, recorded above), many females are still in their cocoons; if too late, many will have left the nest. Since the colony is part of an annual cycle, the figures for productivity should be divided by 365 to obtain a comparison with the Polybiine estimate of 0.063 queens per queen per day. The figures so arrived at are: 0.077, 0.083, 0.078, 0.46 and (0.1). Except for *V. germanica*, the estimates are not so much higher as might have been expected, considering the hazards of hibernation in a temperate climate. The queens of VESPINÆ have six ovarioles on each side, instead of the three found in all the other VESPIDÆ, social and solitary, which have been examined. The large size and eventually greatly enlarged ovaries of the queens make them almost as much superfemales as the workers are reduced females.

The mean sex ratio of the species in Table 31 is 5261 ♂/2736 ♀ = 192.3 ♂/100 ♀, but the accuracy of this estimate is doubtful.

The figures for cells per young queen in the last column but one show the amount of constructive work which is necessary to produce each queen. Possibly species in which this figure is low are better able to survive where the season is short, provided that the productivity is not also too low.

In view of the theoretical discussion on p. 126, it is interesting to see how far the number of queens produced depends on the ultimate size reached by

the colony. This is shown in Table 33, which analyses Weyrauch's figures for *Vespula germanica*.

TABLE 33.

Nests of *V. germanica* arranged according to the number of combs, from Weyrauch (1935).

No. of combs	No. of nests	Mean no. of young queens	Mean date of examination
5	2	0	25.viii.
6	3	107	19.ix.
7	4*	125	20.ix.
8	3	173	17.ix.
9	3	213	22.ix.
10	2*	100	30.viii.

* One of these nests contained no young queens.

The figures show that the two smallest and two largest nests were taken too early for the full number of young queens to be present. Apart from this, however, there is a fairly close relation between the number of young queens produced and the number of combs, on the average 20.6 queens per comb. The queens are, of course, produced from special large cells in the lowest combs, but the number of queen cells probably depends on the number of workers and therefore on the number of cells in the nest as a whole.

17. THE FUNDAMENTALS OF SOCIAL LIFE.

A large step towards social life can be taken by any solitary species by rearranging the elements of which nest-making is composed. In completely solitary species, such as most POMPILIDAE, cells are made one at a time and are stored, layed in, and closed before another one is constructed, not necessarily at an adjacent site. The next stage, the aggregation of cells into a small volume or compound nest, is seen in most solitary bees and wasps. The probable advantages are the full exploitation of a limited area favourable for nesting and possibly some measure of protection for the earlier cells while the later ones are being constructed. The female, also, will only have to make one locality-study. The third stage is the construction and storing of several cells simultaneously, instead of completing one cell before starting another. This is a mere rearrangement of duties, and would be unlikely to reduce the labour involved. It is difficult, therefore, to suggest any clear advantage of the third method over the second, unless, for some reason, the rate of egg ripening makes it inconvenient to separate each egg-laying by the time taken to construct and store a complete cell. Nevertheless, the change has occurred in a number of genera of solitary wasps, e.g. *Amnophila* and several BEMBICIDAE (Sphecoidea) and some *Synagris* (EUMENINAE). With the normal incubation period, the change has a very important effect in that the female comes into direct contact with her larvae in the complete but unclosed cells. Usually these larvae are fed from time to time instead of a sufficient store of provisions being provided before the egg hatches; i.e. there is progressive not mass provisioning.

Up to this stage, the chief advantage of an increase in the length of life of the female is that she will be able to make more cells. This increase in potential reproductive rate is not specifically social, but any additional protection which the earlier cells receive from the continued presence of the female is the first social gain. This function is still of some importance in the old queen of some colonies of the primitive social bees of the genus *Halictus*.

As soon as the third stage has been reached, true social life becomes possible if, and only if,²⁵ the female lives so long that her life overlaps that of her offspring. The contact which she has already had with them as larvae may well provide a valuable conditioning to social behaviour. It appears, therefore, that the second fundamental change necessary for social life is a very considerable increase in the longevity of the female. This could only be avoided by the provision at intervals of "substitute queens," rather in the manner of termites.

With progressive provisioning, where the demands made by the larva probably partly determine how much food it receives, conditions are particularly favourable for the production of "over-fed" and therefore perhaps longer-lived females. It is probably only under tropical²⁶ conditions where more or less continuous breeding is possible that the longer life of the female could quickly lead to social developments. In temperate climates the season would be so short that, without the great specialisations which the social wasps of these regions exhibit, the colony could hardly develop. Everything points to social life as a development of the tropics; the invasion of the temperate regions probably came relatively late and was made by forms in which the social habit was already well established.

Real social life first appears when the mother and her offspring (or, less probably, a number of sisters) co-operate in making a nest and feeding their young. The best criterion is that a wasp should feed a larva derived from the egg laid by another individual or help to construct its cell.²⁷

The exact way in which the worker caste first arose is uncertain. In the Hymenoptera the caste is very distinct morphologically only in the ants, in *Apis* and in the allied MELPONIDAE (stingless bees). In *Vespa* (s.l.) it is much more distinct in some species than in others, and intermediates sometimes occur in the later summer. In *Polistes*, and even more in the POLYBINA, differentiation is very slight and mainly a question of function. It appears, at least in the VESPIDAE and in *Bombus*, that the failure of the worker ovary to develop is due to an inhibition exerted by the presence of an egg-laying queen. Pardi's interesting observations on the psychological dominance of the queen in *Polistes* have already been referred to. This state of affairs may

²⁵ There appears to be very little evidence that social life started from an association of sisters in the absence of the mother. Where this appears to happen in some *Polistes* or *Belonogaster*, it is probably a secondary development in forms which have long been truly social.

²⁶ It might be suggested that the prolongation of the life of the female was originally merely an extension of the already long life of such forms as female *Halictus*, which pass the winter as a resting fertilised female. Various solitary wasps, such as *Anoplius fuscus* (L.) (POMPHILIDAE) and *Ancistrocerus nigricornis* (Curt.) (= *callosus* Thoms.) (EUMENINAE), hibernate in the same way. Nevertheless, the zoogeographical evidence in favour of the tropical origin of the social habit in the VESPIDAE is extremely strong.

²⁷ A nest with a communal principal entrance is known in some species of *Andrena* (solitary bee) and *Metacrabro* (Sphecoidea).

well be the result of a long evolutionary process. Originally, the suppression of oviposition in most of the females may have been due to even more active intolerance on the part of the female which happened first to be ready to lay eggs.

Another outstanding feature of social Hymenoptera is the elimination of the male from the early stages of the colony. In solitary species, the eggs laid by the female produce approximately equal numbers of males and females. In social species, though at the end of the reproductive cycle a similar sex ratio may be observed, there is a preliminary period in which only females are produced. Although the males are produced from unfertilised eggs, they appear rather before or at the same time as the young queens; their production is not due therefore to the exhaustion of sperm in the spermatheca of the old queen. There must be some stimulus from the state of the colony, or from the age of the queen which leads her to lay male-producing eggs.

Finally, it seems necessary to assume that social forms have retained, or acquired, a greater plasticity of behaviour than is now shown by most solitary species. This is most marked in the ants, but is evident even in the wasps, in some ways the least advanced of the three main groups of social Hymenoptera.

Assuming, then, that a social life has been evolved by steps which are still obscure, we have a colony of the following type: (a) one or more egg-laying queens; (b) workers, usually considerably more numerous, produced successively in the first part of the life of the colony; (c) eventually numbers of young queens and males, and, at any rate in what is probably the more primitive condition, the colony breaks up. Assuming that the original queen or queens have completed their task and that the males die soon after fertilising the young queens, the first problem is the most efficient way to partition the workers and young queens for the founding of new colonies. The measure of efficiency is "queens per queen per day," *i.e.* how many young queens are produced by each original queen in how many days. This problem and several cognate ones may be analysed algebraically.²⁸

Let a colony be started by q founder queens and p founder workers. Assume, for preliminary calculations, that the queens take no part in building but that they can supply sufficient eggs to fill every cell as soon as it is constructed or vacated (*i.e.* egg supply is never a limiting factor). Cells are used again and again until the end of the colony.

Let the average length of life of the worker be s days. It is assumed that equal numbers of founder workers emerged each previous day in the mother colony, so that a fraction $1/s$ will die each day in the new colony.

Let the average developmental period (temperature fluctuations being ignored) from egg to adult be d days.

s must be $> d$, or true social life is scarcely possible. It will be assumed, for convenience in calculation, that $d < s < 2d$ and let $t = s - d$, so that $d + t = s$, $t > 0$. Such a value for s is not unreasonable, and does not materially alter the nature of the conclusions. Any initial period in which immature workers do not work may be regarded as included in d rather than in s ; similarly, any non-working period at the end of life may be regarded as excluded from s .

²⁸ The analysis of the problem by Bodenheimer (1937) is too generalised for present purposes.

Let each worker, on the average, add r cells to the colony a day. This is a mathematically convenient abstraction. In practice, there is a considerable division of labour amongst the workers. Moreover, building, nursing and foraging activities often alternate, so that the average rate of building for the whole life of the colony is much less than the maximum rate when building is the principal activity. The figure r cells a day is an average figure for all workers (including those doing no building) and for the whole life of the colony (including times when workers are not engaged in building).

A generation of workers is defined as those which emerge in a period of d days. Thus the founder workers form Generation 0 (= Gen. 0). Gen. 1 emerges between days $d + 1$ and $2d$ inclusive. Gen. 2 between days $2d + 1$ and $3d$, etc. The lives of the generations overlap considerably, since the first of Gen. 1 emerge on day $d + 1$ and are dead on day $2d + t + 1$ ($= s + d + 1$), whereas the last of Gen. 1 emerge on day $2d$ and are dead on day $3d + t + 1$. Thus some of Gen. 1 are contemporaneous with Gen. 0 and others with Gen. 4.

For economy in presentation the following abbreviations will be used.

R_x = larva/worker ratio on day x .

E_x = efficiency of a colony in which laying of queen eggs starts on day x and ends on day $x + d$.

$$N_{x-1} = pr \left(x - \frac{x(x+1)}{2s} \right).$$

$$N_{x-2} = pr^2 \left(\frac{x(x+1)}{2} - \frac{x(x+1)(x+2)}{2.3.s} \right).$$

$$N_{x-n} = pr^n \left(\frac{x(x+1) \dots (x+n-1)}{n} - \frac{x(x+1) \dots (x+n)}{s \cdot n+1} \right).$$

The method used below is an approximation, dividing the life of the colony up into one-day periods, but it appears sufficient to demonstrate the general form of the results. The progress of the colony from day 1 to day $3d$ is shown in Tables 34-36.

The expression for the accumulated number of cells becomes increasingly inelegant, chiefly owing to the endeavour to build a model which has some resemblance to reality. It may be noted, however, that, provided r is considerably greater than $\frac{1}{d}$, far the largest term in the expression for the number

of cells after nd days is N_{d-n} .

It seems that one of the most critical factors in the development of the colony is the larva/worker ratio, especially in the period up to day d and specifically on that day, when many founder workers have died and no new ones have yet emerged. It will be seen in the numerical example given in Table 37, that the ratio rises to a high value at day d and thereafter fluctuates about more reasonable levels.²⁹ The value of the larva/worker ratio on day d , = R_d , may be calculated as follows, assuming, as on p. 10, that the egg, larval, and pupal stages occupy 0.2, 0.4, and 0.4 of d respectively.

²⁹ In all the nests for which we were able to calculate the ratio (12 species), its value lay between 0 and 6.8, usually below 4.0 (see Table 27).

TABLE 34.
Growth of colony from day 1 to day d .

	Day			
	1	2	t	$t+1$
Gen. 0 ♂, alive	$p\left(1 - \frac{1}{s}\right)$	$p\left(1 - \frac{2}{s}\right)$	$p\left(1 - \frac{t}{s}\right)$	$p\left(1 - \frac{t+1}{s}\right)$
Cells constructed	$pr\left(1 - \frac{1}{s}\right)$	$pr\left(1 - \frac{2}{s}\right)$	$pr\left(1 - \frac{t}{s}\right)$	$pr\left(1 - \frac{t+1}{s}\right)$
Cells accumulated	$N_{1,1}$	$N_{2,1}$	$N_{t,1}$	$N_{t+1,1}$
				d
				$p\left(1 - \frac{d}{s}\right)$
				$pr\left(1 - \frac{d}{s}\right)$
				$N_{d,1}$

TABLE 35.
Growth of colony from day $d+1$ to day $2d$.

	Day			
	$d+1$	$d+2$	$d+t$	$d+t+1$
Gen. 0 ♂, alive	$p\left(1 - \frac{d+1}{s}\right)$	$p\left(1 - \frac{d+2}{s}\right)$	0	0
Cells constructed	$pr\left(1 - \frac{d+1}{s}\right)$	$pr\left(1 - \frac{d+2}{s}\right)$	0	0
Cells accumulated	$N_{d+1,1}$	$N_{d+2,1}$	$N_{d+t,1} = N_{s,1}$	$N_{t+1,1}$
Gen. 1 ♂, emerged (= cells constructed + cells vacated d days before)	$pr\left(1 - \frac{1}{s}\right)$	$pr\left(1 - \frac{2}{s}\right)$	$pr\left(1 - \frac{t}{s}\right)$	$pr\left(1 - \frac{t+1}{s}\right)$
Gen. 1 ♂, accumulated	$N_{s,1}$	$N_{s,1}$	$N_{t,1}$	$N_{t+1,1}$
Cells constructed	$rN_{1,1}$	$rN_{2,1}$	$rN_{t,1}$	$rN_{t+1,1}$
Cells accumulated	$N_{1,2}$	$N_{2,2}$	$N_{t,2}$	$N_{t+1,2}$
Total of all cells accumulated	$N_{d+1,1} + N_{1,2}$	$N_{d+2,1} + N_{2,2}$	$N_{s,1} + N_{t,2}$	$N_{s,1} + N_{t+1,2}$
				$N_{d,1}$
				$rN_{d,1}$
				$N_{d,2}$
				$N_{s,1} + N_{d,2}$

TABLE 36.—Growth of colony from day $2d + 1$ to day $3d$.

	Day			
	$2d + 1$	$2d + 2$	$2d + t$	$2d + t + 1$
Gen. 1 ♂, accumulated	N_{d+1}	N_{d+1}	N_{d+1}	$N_{d+1} - N_{d-t+1}$
Cells constructed	rN_{d+1}	rN_{d+1}	rN_{d+1}	$rN_{d+1} - rN_{d-t+1}$
Cells accumulated	$N_{d+2} + rN_{d+1}$	$N_{d+2} + 2rN_{d+1}$	$N_{d+2} + trN_{d+1}$	$N_{d+2} + \frac{t+1}{N_{1+2}}rN_{d+1} - N_{d-t+2}$
Gen. 2 ♂, emerged (= cells constructed + cells vacated d days before)	$pr\left(1 - \frac{d+1}{s}\right) + pr\left(1 - \frac{1}{s}\right) + pr^2\left(1 - \frac{1}{s}\right)$	$pr\left(1 - \frac{d+2}{s}\right) + pr\left(1 - \frac{2}{s}\right) + pr^2\left(2 - \frac{2.3}{2.8}\right)$	0 $+ pr\left(1 - \frac{t}{s}\right) + pr^2\left(t - \frac{t(t+1)}{2.8}\right)$	$pr\left(1 - \frac{d}{s}\right) + pr^2\left(d - \frac{d(d+1)}{2.8}\right) + pr\left(1 - \frac{t+1}{s}\right) + pr^2\left(t+1 - \frac{t+1(t+2)}{2.8}\right)$
Gen. 2 ♂ accumulated	$pr\left(1 - \frac{2d+2}{2s}\right) + N_{1+1} + N_{1+2}$	$pr\left(2 - \frac{4d+6}{2s}\right) + N_{2+1} + N_{2+2}$	$pr\left(1 - \frac{2d+t+1}{2s}\right) + N_{t+1} + N_{t+2}$	$pr\left(1 - \frac{2d+t+1}{2s}\right) + N_{d+1} + N_{d+2}$
Total of all cells accumulated	$N_{s+1} + N_{d+2} + rN_{d+1} + N_{1+2} + N_{1+3} + pr^2\left(1 - \frac{2d+2}{2s}\right)$	$N_{s+1} + N_{d+2} + 2rN_{d+1} + N_{2+2} + N_{2+3} + pr^2\left(\frac{2.3}{2} - \frac{2.3.d + \frac{2.3.4}{3}}{2s}\right)$	$N_{s+1} + N_{d+2} + trN_{d+1} + N_{t+2} + N_{t+3} + pr^2\frac{t(t+1)}{2} + \left\{1 - \frac{3d+t+2}{3s}\right\}$	$N_{s+1} + N_{d+2} + drN_{d+1} - N_{d-t+2} + N_{d+2} + N_{d+3} + pr^2\frac{t(t+1)}{2} + \left\{1 - \frac{3d+t+2}{3s}\right\} + \frac{d - tpr^2}{1 - \frac{2d+t+1}{2s}}$

TABLE 37.

Growth of wasp-colony and course of larvae/worker ratio. Assumptions: $p = 90$, $s^* = 45$, $d = 30$, $t = 15$, $r = 0.5$, egg-stage = 6, larval = pupal stage = 12 days; oviposition not a limiting factor. Number of larvae up to day 6 = 0; day 7 to day 18 = $N_{1,1}$, $N_{2,1}$, . . . $N_{12,1}$; day 19 to day 30 = $N_{12,1} - \bar{N}_{1,1}$, . . . $N_{24,1} - N_{12,1}$; after day d , the number of larvae can be calculated from a careful examination of Tables 35 and 36.

	Day											
	1	2	15	16	20	25	30	31	32	45	60	90
No. of cells	44	87	555	584	690	800	885	921	977	3350	8972	74787
No. of larvae	0	0	360	395	438	378	318	306	294	1060	3880	35554
No. of ♂	88	86	60	58	50	40	30	72	113	555	885	9302
R. . .	0	0	6.00	6.78	8.76	9.45	10.60	4.25	2.60	1.91	4.38	3.82

* Values for s and d have been chosen to simplify the arithmetic.

The number of workers on day d is $p \left(1 - \frac{d}{s}\right)$. The number of larvae equals the number of cells on day $0.8d$ less the number of cells on $0.4d$ ($0.4d$ can always be made a whole number by choosing an appropriate time-unit).

This is $N_{0.8d,1} - N_{0.4d,1} = 0.4prd \left(1 - \frac{1.2d + 1}{2s}\right)$.

$$\text{Thus, } R_d = \frac{0.4rd \left(1 - \frac{1.2d + 1}{2s}\right)}{1 - \frac{d}{s}}.$$

The following conclusions may be drawn from this expression:

(a) R_d is independent of p , the number of founder workers. This is evidently true at all periods in the life of the colony.

(b) R_d increases indefinitely with r .

(c) R_d increases indefinitely with d , provided $\frac{d}{s}$ is constant.

(d) R_d has a limiting value of $0.4rd$ as s is increased relative to d . This is in fact the value it would have if no founder workers died before day d .

Any difficulties which these conditions might give rise to are probably solved in nature by temporal variations in the value of r , which is not in fact independent of the oviposition-rate.

The next general conclusion concerns the partition of workers. The expression for the number of cells in a colony contains p only as a simple multiple. Therefore two colonies founded by $\frac{p}{2} + x$ and $\frac{p}{2} - x$ workers, respectively, will, in a given time, have the same number of cells as a single colony founded by p workers. Thus, the number of founder workers is only important if secondary considerations are examined, e.g. the time for the colony to pass a certain minimum size which may affect temperature control (p. 128) or defence against enemies (p. 127).

Again, for all probable³⁰ values of r , d , and s , the number of cells in the colony grows extremely rapidly (Table 37), especially after day $2d$. As has already been suggested, it is almost certainly as necessary as it is reasonable to postulate variation in the value of r . But it may be significant that the Polybiine wasps in British Guiana appear to fall into two groups, those in which the colony breaks up before day $3d$, and those in which it is potentially perennial, r eventually approaching zero.

At some point in the life of the colony, eggs which will produce males and females must be laid in some of the cells. Suppose on day d , growth of the nest ceases, and as cells become vacant they have deposited in them eggs to produce workers, males and females in the right proportions, that is, so that at the end of the process they shall be in the proportions of $p : q : q$. After day $2d$ there is no more oviposition and the last adult emerges on day $3d$. The measure of efficiency, E_d , is the number of new queens per old queen per day. The mean date on which the queens are produced can be calculated, but it is a very complicated expression; greater simplicity, with no important inaccuracy is achieved if all the queens are ascribed to day $3d$, when the last one emerges (the true figure lying between $2d$ and $3d$).

On day d there are $N_{a,1}$ cells so that in the last cycle this number of ♀, ♂ and ♀ will be produced, but there will also be workers surviving from Gen. 1, namely those which emerged between days $2d - t$ and $2d$. This number is $N_{a,1} - N_{\bar{a}-t,1}$. Thus, in order that the castes should be produced in the right proportions, suppose of the final $N_{a,1}$ wasps, $(1 - 2a)N_{a,1}$ are workers and $2aN_{a,1}$ are males and queens. Then:

$$\frac{(1 - 2a)N_{a,1} + N_{a,1} - N_{\bar{a}-t,1}}{2aN_{a,1}} = \frac{p}{2q}.$$

So that
$$a = \frac{q}{p + 2q} \cdot \frac{(2N_{a,1} - N_{\bar{a}-t,1})}{N_{a,1}}.$$

On any day in the last cycle $1 - 2a$ of the wasps are workers, a are males, and a are queens. The efficiency of the process is therefore,

$$E_d = \frac{aN_{a,1}}{3q \cdot d} = \frac{1}{3(p + 2q)} \cdot \frac{2N_{a,1} - N_{\bar{a}-t,1}}{d}.$$

By a similar argument, the efficiency of a queen-producing cycle of d days, starting on day $2d$, is:

$$E_{2d} = \frac{1}{4(p + 2q)} \cdot \frac{2N_{a,1} + 2N_{a,2} - N_{\bar{a}-t,1} - N_{\bar{a}-t,2}}{d}$$

where $N_{\bar{a}-t,1} = N_{s,1}$ if $d - t > t$, that is $t < \frac{d}{2}$.

In general, in determining $E_{n,d}$, the largest term in the expression will be $N_{a,n}$, and the value of $E_{n,d}$ will mainly depend on its magnitude.

This term is $\frac{pr^n d : \bar{d} + 1 \cdot \cdot \cdot \bar{d} + n - 1}{\lfloor n} \left(1 - \frac{d + n}{(n + 1)s}\right)$. The negative

³⁰ The mean value of r in 33 nests of 8 species (Table 24) was 0.67; d may be about 21 days (p. 116); s is quite unknown, but almost certainly lies between 28 and 49 days.

term approaches a limit of $\frac{1}{s}$ as n gets larger. The positive term will increase as long as $\frac{r(d+n-1)}{n}$ is > 1 . If

$$\frac{r(d+n-1)}{n} = 1, n = \frac{r(d-1)}{1-r}.$$

Thus, if $d = 21$ and $r = 0.5$, n would equal 20. Thus, provided oviposition is not a limiting factor, $E_{n,a}$ is unlikely to decrease (apart from secondary considerations) before a much longer period has elapsed than need be considered.

It is now possible to bring in the fact, demonstrated in Table 24, that the value of r depends on q , the number of queens. If d has a value of 21 days, then $r = (119q + 3986)10^{-4}$; assume, also, that $s = 35$ days. It was shown in Table 28 that the average composition of young colonies of 20 colonies of 8 short-cycle species was 15.9 queens and 93.8 workers + intermediates. Thus $p + 2q = 125.6$. To simplify the arithmetic and to allow for the deaths of some workers, assume that $p + 2q = 130$, so that $p = 130 - 2q$. Substituting these values, the following equation is obtained:

$$E_a = \frac{10^{-6} \cdot 226}{39.21} \{518180 + 7498q - 238q^2\}.$$

To find the value of q , for which E_a is maximum, differentiate for q and equate to zero.

$$476q = 7498, q = 15.75$$

The calculated values are compared with the observed ones in Table 38. The corresponding calculated and observed values for $d = 30$ and $s = 45$ have been added.

TABLE 38.

Comparison in short-cycle POLYBIINAE of observed values and those calculated for maximum reproductive efficiency. (a) $d = 21$, $s = 35$; (b) $d = 30$, $s = 45$.

Variable	q		r		E_a	
Assumption	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>
Observed		15.9	0.666	0.466	0.063	0.044
Calculated	15.75	16.0	0.586	0.412	0.159	0.093

The agreement is probably sufficiently good considering the assumptions which were made in estimating even the observed values of r and E_a .

A similar calculation for $E_{2,a}$ ($d = 21$, $s = 35$, $p + 2q = 130$) gives the following values: $q = 41.24$ (the other value of q is negative and therefore biologically impossible), $r = 0.889$, and $E_{2,a} = 1.057$. This shows what a large proportion of queens would be necessary to maintain construction at the rate at which it starts.

Finally, it may be noted that if r is a linear function of q , then the expression for E_a is made up of constants (depending on d and s) and an expression of the type $\frac{p(aq+b)}{p+2q}$. This will increase indefinitely as $p + 2q$ increases.* Thus, on these assumptions, efficiency increases with the size of the founder group.

* p and $q > 1$; ratio $p:q$ constant.

No doubt the physical properties of the nest would be a limiting factor, apart from any other consideration; for a large founder group to be efficient, it would have to build a very large nest.

This argument can be extended to cover the partition of the whole group of workers and queens to which a colony starting a queen-cycle on day d would give rise. The measure of efficiency is an expression of the type $C \frac{p(aq + b)}{p + 2q}$, where C is a constant.

Suppose the original colony gives rise to mn sets of $p + 2q$ workers, queens and males. The total reproductive efficiency of the m colonies founded by sets of n ($p + 2q$) wasps is $m \left[\frac{Cnp(aq + b)}{n(p + 2q)} \right] = \frac{Cp}{p + 2q} [amnq + mb]$. If mn is fixed, the efficiency increases indefinitely with m , that is with largest number of the smallest possible colonies. Thus, a colony with a large founder-group is always relatively more efficient than one built by a similar but smaller group, but when the number of wasps is limited, it is better to divide them into as many sets as possible.

It can easily be appreciated that the larva/worker ratio will tend to decrease if the life of the worker is longer than the larval period, since the difference will lead to a relative accumulation of the workers. But any check to oviposition will decrease the ratio even more sharply. Thus the type of queen-cycle which has been assumed (in which oviposition ceases when all queen-producing eggs have been laid) would greatly reduce the ratio towards the end of the life of the colony. This might be the chief mechanism in differentiating the queens from workers.

There are several contingencies which might modify the assumptions hitherto made. The number of queens has been shown (p. 103) to control the oviposition rate of each one. A high oviposition rate might shorten the life of the queen, and this might well be an important consideration in species of the long-cycle type. There is, again evidence in most social insects (ants, termites, *Bombus*, *Vespa*, but not *Apis*) that prolonged oviposition at a high rate reduces the mobility of the queen; in *Vespa* and *Bombus* the old queens are no longer capable of flight. If in the tropics, as suggested earlier (p. 97), ants, especially Driver Ants, are important enemies of wasps, this will favour colonies with a high proportion of queens. For such queens will retain their mobility much longer, and if ants do raid such a colony it will be possible afterwards to maintain a very high oviposition rate for a short period. Thus a new colony might be restocked with eggs very rapidly, as described in *Parachartergus fraternus* (Grib.) (p. 82).

While a high mobility and potential oviposition rate may be the best defence against ants, it is probable that resistance to vertebrate enemies will depend very largely on the size of the colony. The size of the founder group determines the time taken for the colony to reach a given size. If vertebrate enemies were important it might pay to found colonies with large groups so as to pass through the dangerous small size more quickly. But with intense predation of a type to which resistance was rarely successful a small, short-lived colony might be more efficient. It is impossible to say whether enemies would more easily find a few scattered colonies or a large number of much smaller ones.

The size of a colony will also determine the temperature at which it can be maintained. Heat production depends on the number of inhabitants (*i.e.* roughly on the volume) while heat loss depends on the surface, so that large colonies will, in this respect, be more efficient. The actual temperatures reached will depend on the physical properties of the nest; modifications of the envelope, especially the construction of additional layers separated by air, would be very important. At a higher temperature oviposition and the development of the early stages will be more rapid, so that the process is to some extent autocatalytic. These facts have recently been made use of in the cultivation of honey-bees in the so-called "skyscraper" hives (Dugat, 1947), in which several colonies are placed on top of one another, with passages allowing the movement of air or of workers, but not of the queens (which would fight). It seems clear that most of the success of this method is due to the high temperatures reached, though there is an additional advantage from a more efficient division of labour amongst the workers. In the POLYBIINAE it has been suggested (Ducke, 1914: 323) that such species as *Polybia occidentalis* (Oliv.) build larger nests at the edge of the tropics than they do in the rain forest. It seems probable that this is related to the maintenance of a tolerable temperature in the cool winters. Ducke also notes (*loc. cit.*: 324) that species such as *Polybia occidentalis* and *Protopolybia sedula* (= *P. minutissima* (Spin.) var. *sedula* (Sauss.)) store much more honey in subtropical regions and this may well serve the same purpose.

In temperate regions colonies are annual and, though climate probably does not directly determine the dissolution of the individual colonies, the arrangement is clearly adapted to meeting the difficulties of a period of low temperature and food shortage. The haplometrotic condition (one egg-laying queen), absence of swarming, and (especially in *Vespa s.l.*) the greater divergence of the castes are probably all adaptations to hibernation. The queen has to be supplied with a large enough fat-body to exist for several months without food. She has developed, therefore, into what might be regarded as a "superfemale" at the expense of the workers. In this respect, the genus most worthy of study is *Polistes* which, in N. and C. Europe, is strictly haplometrotic, but in N. Africa (Weyrauch, 1939: 178) may found colonies by swarming. In N. Italy (Pardi, 1942) occurs a curious arrangement under which several queens may unite to found a colony though only one of them ultimately survives. Unfortunately, the development of the worker caste in this genus in different parts of its range has not yet been studied. It is possible that this genus will ultimately supply the key to many of the problems of social evolution.

The winter rest of the queens in *Vespa*, etc., seems to have introduced a new factor, namely an inhibition of ovarian development in young autumn queens. Thus a developed ovary in the autumn may, as in *Bombus*, actually be much more characteristic of workers than of young queens. A similar inhibition, associated with the accumulation of a store of fat, is known in several other hibernating insects (Rhynchota, Diptera).

The factors considered in the preceding paragraphs will perhaps go a long way in accounting for the different types of colony found in the VESPIDAE. It is still uncertain, however, whether they can account for the small size of most *Mischocyttarus* colonies. This may perhaps be due to some peculiarity

in the physiology of the female ovary combined with a relatively short life. As both the larva and, in many ways, the adult of *Mischocyttarus* seem to be specialised, it is not clear whether the genus is derived from ancestors less adapted to social life or is a degenerate type. The genus is richer in species than any other Polybiine, but less numerous in individuals, chiefly because of the scarcity of workers (Richards, 1945 : 300).

Although speculations of the type put forward in this section might be pushed further, it is probably best to wait until further observation has obtained more certain values for some of the constants. It is necessary, in particular, to know the durations of the three stages of the developmental period, to have more accurate censuses of nests of various ages, to know the mean length of the life of the wasps, and to know more of the composition of founder swarms.

18. APPENDIX 1.

By O. W. RICHARDS.

The species of *Polybia* allied to *P. occidentalis* (Oliv.).

Most of Central and South America is inhabited by a complex of closely allied forms which Ducke (1910 : 406) treated as a single variable species. The variations in structure and behaviour are, however, so marked that this course is clearly unsatisfactory, though an easily workable alternative is hard to find. No two nests, even of what is clearly one species, have completely similar populations, and some nests are strikingly aberrant. There is also considerable, though often not very clear-cut, geographical variation.

In the preliminary study of an exotic fauna there is much to be said for the principle of confining the term species to groups with well-defined structural differences. But it must be clearly recognised that this principle is not based on any fundamental biological truth. With some knowledge of their biology, social insects provide unusually favourable material for deciding whether or not forms which hardly differ in structure (e.g. *Bombus terrestris* (L.) and *B. lucorum* (L.), in Europe) should be treated as species or of lower status. The essential criterion in sympatric groups is whether the gene-flow between them is either free or absent or much impeded. This can usually be decided by examining nest-populations. However close two forms are structurally, if they are always found in different nests the presumption is high that they belong to different species.

Nest-populations are also of great value in the biometrical analysis of critical species, since they give one a measure of the amount of variation to be expected amongst individuals which certainly belong to one species. On the other hand, the characteristics of a species for taxonomic purposes are best drawn up from a sample of as many separate nests as possible, since each single nest is sure to be in some respects abnormal. All the mean ratios enumerated below were calculated from samples drawn from as many nests as possible (unless otherwise stated).

In the analysis of the allies of *P. occidentalis* a number of measurements have been made with a screw-eyepiece micrometer (187 units = 1.0 mm.), and most of the results are expressed as ratios. In a few cases the absolute measurements are also useful.

(1) OOL : POL ratio.

The distance between the outer edge of a lateral ocellus and the nearer compound eye, divided by the distance between the inner edges of the two lateral ocelli.

(2) Hind-wing ratio (figs. 11 and 12).

The distance along vein Cu 1, measured from the slight kink near where it joins vein 2A to the centre of the basal sector of M4, divided into the distance (along a straight line across the arc) between the centre of the basal sector of M4 and the point where M4 reaches the wing-margin.

(3) Eye/tempora ratio (fig. 13).

When the head is viewed from the left, held so that the base of the left antenna is just hidden by the left eye, the width of the eye divided by the width of the tempora (both in optical section). The ventral margin of the tempora taken either as the temporal furrow or, in species where this is absent, as a tangent to the profile of the more dorsal part of the tempora.

(4) 1st tergite ratio (fig. 14).

The length of the 1st tergite divided into its posterior width. The length was measured in side view in two parts, *viz.* from the posterior end of the dorsal muscle to the centre of the spiracle, and from the centre of the spiracle to the centre of the posterior margin. The ratio of these two length-measurements was not found to be very useful in distinguishing species, so they were added together and only the total length was used. The ratio is normally larger (*i.e.* 1st tergite broader) in queens than in workers, but queens are only likely to be available in nest-populations.

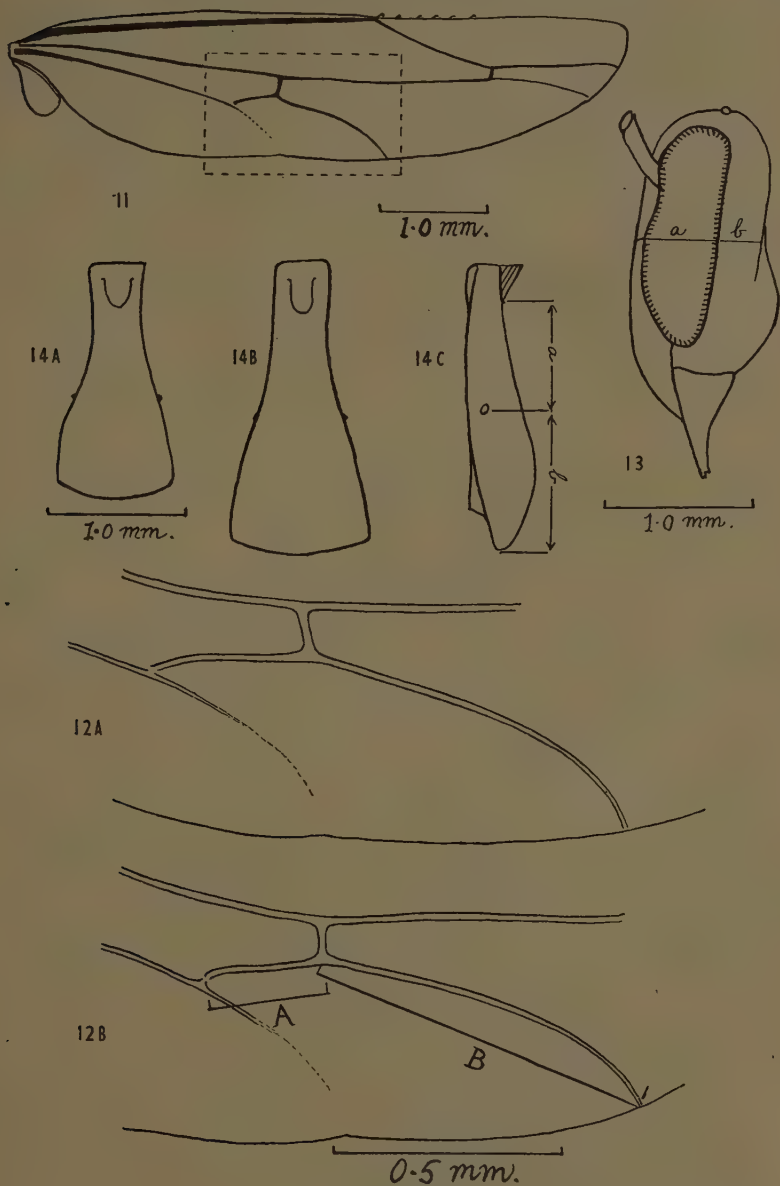
The absolute length and width of the 1st tergite are also characters of some importance.

(5) The length of the fore-wing, measured to the nearest half millimetre and the number of hamuli (hooks) on the hind-wing were also recorded.

Probably another worker would find it difficult to reach the same estimates of the ratios, but he would probably arrange the species in the same order. This difficulty can only be overcome by determining the personal factor, by making measurements in part on specimens from some of the areas which were the source of the material studied here.

Under the arrangement first proposed by Bequaert (*in* Rau, 1933 : 314), and extended in Bequaert (1944), two species are recognised, *viz.* *Polybia bistriata* (Fab.), with no temporal keel and generally paler ground-colour, and *P. occidentalis* (Oliv.), with a temporal keel and generally black ground-colour. Bequaert also recognises a number of "varieties" of *P. occidentalis* differing only in colour or sometimes also in average size. Some of these varieties have a restricted geographical distribution (*i.e.* are probably subspecies) but others of them appear to occur together in one district.

The reasons for subdividing these two species further were primarily biological, that is, we noticed differences in the type of nest, size of cell, percentage of queens, etc. This led to a search for structural differences between the forms, and these have been found, at least in the Guiana material. The



FIGS. 11-14.

- FIG. 11. Hind-wing of *Polybia bicyttarella* Rich., showing region of taxonomic importance.
 12. Hind-wing ratios; (a) *Polybia bicyttarella* Rich., (b) *P. bistrata* (Fab.). The ratio = B/A .
 13. Side view of head of *Polybia occidentalis* (Oliv.). The eye/tempora ratio = a/b .
 14. First abdominal tergite; (a) *Polybia parvula* (Fab.), dorsal view, (b) *P. occidentalis* (Oliv.), dorsal view, (c) the same, lateral view.

differences show some overlap but are statistically significant and would always be detectable in samples of, say, ten specimens. It seemed desirable to carry the analysis somewhat further and study material from other parts of S. and C. America. The aim was to distinguish (1) a number of species differing, at least on the average, in structure and having, usually geographical, ranges which overlap widely, (2) subspecies which differ, often, in colour only, but whose ranges do not or scarcely overlap. A complete revision of the forms hitherto included under *P. occidentalis*, however, would be a major work and would require many nest-populations and information as to the details of nest structure and biology which are not at present available. It has seemed best, therefore, to recognise those species and subspecies which can at present be distinguished and to call the remaining forms "varieties" of *P. occidentalis*; some of these, such as the var. *scutellaris* (White), will probably later be shown to be species. The relatively satisfactory way in which the more northern species have sorted out suggests that critical field-work may ultimately settle the classification of the species in the southern part of its range.

1. *Polybia bicyttarella* sp. n.

Very close to *P. bistriata* (Fab.) and like that species with no, or extremely feeble, temporal furrow but with a small hind-wing ratio. In colour closely resembling the paler form of *P. bistriata* (Fab.).

Female. Temporal keel not developed; ventral half of the clypeus usually with traces of an impressed central line; hind-wing ratio (fig. 12a) (material from 8 nests) 2.07-2.91, mean 2.57; OOL:POL, 2.15-3.08, mean 2.56; eye/tempora ratio 1.43-2.11, mean 1.70; length of fore-wing 6.0-7.0, mean 6.80 mm.; number of hamuli 5-8, mean 6.83; general colour light brownish-yellow; clypeus with a ventral U-shaped yellow band which meets, or almost meets, the yellow spots on the inner orbits which entirely fill the ocular sinus; outer orbits yellow; inner dorsal edge of antennal socket with a yellow spot; pale spot behind lateral ocelli, if present, indefinite and tending to form a circle rather than an oblique line; pronotum with a moderately broad yellow band and a long yellow streak in front of the ventro-lateral prominence; mesonotum with 2 median and 2 shorter lateral yellow stripes; mesopleuron with a yellow streak from the pronotal tubercle to, or nearly to, the metapleural suture below the punctiform fovea; scutellum with 2 large yellow spots on each side or with an emarginate band; postscutellum with 2 large yellow spots; propodeum with 2 large yellow spots; abdomen with narrow yellow bands on tergites 1-4; pattern rather constant.

Male. Clypeus shorter and more obtuse than in female, with short silvery pubescence; tempora much narrower than in female; 7th sternite flattened; penis valves with distal part squarer, sides less converging than in *P. bistriata* (Fab.) (fig. 16b). In addition to

EXPLANATION OF FIGURES 15-24.

- Fig. 15. Ventral view of right half of genitalia of *Polybia diguetana* R. du Buyss., ♂.
 16. Dorsal view of tip of aedeagus of (a) *Polybia bistriata* (Fab.), (b) *P. bicyttarella* Rich., (c) *P. occidentalis* (Oliv.).
 17. Right volsella of *Apoica arborea* Sauss., ♂, dorsal view.
 18. Aedeagus of same species, dorsal view.
 19. End of right paramere of same species, dorsal view.
 20. Right volsella of *Apoica pallida* (Oliv.), dorsal view.
 21. Aedeagus of same species, dorsal view.
 22. End of right paramere of same species, dorsal view.
 23. Aedeagus of *Apoica pallens* (Fab.), form A, dorsal view.
 24. The same, of form C.



FIGS. 15-24.

parts which are pale yellow in female the following areas are also that colour: area above clypeus to a little above antennal sockets; almost whole mesopleuron and mesosternum; all coxae beneath, and most of anterior femur and tibia; anterior bands on both scutellum and postscutellum; bands on abdominal tergites 1-6; large posterior spot on tegulae.

Biological characters:—Initial colony (p. 9) 1-2 combs, 100-300 cells; final colony 3 combs, 500-600 cells; length of cells 6.5-7.0 mm.; diameter of cells 2.85 mm.; cocoons projecting 3.0 mm. beyond the rim of the cell; some wasps with the intermediate type of ovary present in 5 out of 10 nests; mean percentage of queens per nest 6.8 per cent.

Type ♀ and allotype ♂, BRITISH GUIANA: Mazaruni Station, clearing, 18.ix.1937, nest 183 (Richards and Smart). Paratypes, all the specimens listed on pp. 59-63 in the account of the biology of the species, and the following in the British Museum Coll.:—British Guiana, ♀ (J. Rodway) (det. as *P. fastidiosuscula*); N.W. district Issororo, vi.1916, ♀ (*G. E. Bodkin*) (British Guiana Dept. Agric.) (see also p. 135, under *P. bistriata* (Fab.)).

This is perhaps the species recorded as *Polybia fulvo-fasciata* by Bodkin (1917). In our collecting in British Guiana, *P. bicyttarella* was found at Mazaruni Station (W. bank of Rivers Essequibo and Mazaruni), where it was about as common as *P. occidentalis*, and on the Kaieteur Savannah, where it was less common than *P. bistriata*. The latter species occurred in Georgetown, at Moraballi Creek (E. bank of Essequibo R.) and was common on the Kaieteur Savannah. A suggestion as to why a distinct species may have evolved at Mazaruni is made on p. 144.

2. *Polybia bistriata* (Fab.).

Polistes bistriata Fabricius [1805].

Polybia oecodoma Saussure, 1854.

P. brunneiceps Cameron, 1912.

Female. Ground-colour nearly always dark brown (but see below); markings as in *P. bicyttarella* sp. n., except for the following differences: a pair of narrow oblique yellow lines behind each lateral ocellus; mark on mesopleuron normally ending at the punctiform fovea. Temporal keel absent or very weak; ventral half of clypeus usually with traces of an impressed central line; hind-wing ratio (fig. 12b) (material from 9 nests) 2.49-3.90, mean 3.07; OOL:POL, 2.06-2.96, mean 2.54; eye/tempora ratio 1.45-2.06, mean 1.77; length of fore-wing 6.0-7.0, mean 6.85 mm.; number of hamuli 5-7, mean 6.25.

Male. Differing in the same structural characters from the female as enumerated for *P. bicyttarella*; distal part of the penis valves laterally converging, trapezoidal rather than square (fig. 16a). Closely resembling female in markings but yellow areas larger; especially clypeus, yellow with variable dorsal black spot on disc; all coxae yellow marked beneath; differs especially from *P. bicyttarella* sp. n. ♂ in the dark mesopleuron with a yellow stripe to below the punctiform fovea and the dark mesosternum.

Biological characters:—Initial colony 1 comb of 200-400 cells; final colony normally 1 comb of 300-500 cells, very rarely 2 combs with *separate entrances* and 600 cells; length of cells 8.0 mm.; diameter of cells 2.65 mm.; cocoons projecting for 1.0-2.0 mm. beyond rim of cell; some wasps with the intermediate type of ovary present in 3 out of 14 nests; mean percentage of queens per nest 13.4 per cent.

The descriptions of *Polistes bistriata* Fabricius [1805], and of *Polybia oecodoma* Saussure, 1854, appear to apply to the present species as far as

colour goes. The types of *P. brunneiceps* Cameron, 1912, from British Guiana (two females, both marked "type"), have been examined in the British Museum collection. It was probably this species which Bodkin (1917) recorded as *Polybia fastidiosuscula* var. *sampaioi*, a species with, in reality, a considerably more eastern distribution.

Besides numerous British Guiana specimens, a large number have been seen from Pará and Manaus in Brazil, and a series from Peru: Valle Chanchomayo (Weyrauch).

There is in the British Museum collection a series of *Polybia* from BRAZIL: Lower Amazons, Itacoatiara, 7.ii.1890, 11 ♀ (*E. E. Austen*) which resemble *P. bicyttarella* in colour except that the pale spots behind the ocelli are a little more definite. The hind-wing ratio, however, is 2.70-4.03, mean 3.11, agreeing closely with *P. bistrriata* (Fab.), of which they must be regarded as a pale form. Three other Brazilian specimens (Amazons; Teffé, 11.vi.1906, ♀ (*Ducke*), ratio 2.83; R. Negro, Manacepruru, vii.1935, ♀ (*G. V. Vredenburg*), ratio 2.42³¹; no precise locality, ratio 3.06) probably belong to the same form. In all 14 specimens the areas round the ocelli and on each side of the yellow mesonotal lines are somewhat blackened, which is not the case in *P. bicyttarella*.

To give some idea of specific variation in the ratios, they have been measured in a number of species more or less closely allied to *P. occidentalis* (Oliv.), and the results are shown in Table 39.

Polybia occidentalis (Oliv.) (*s.l.*).

Bequaert places under this name all the forms which differ from *P. bistrriata* (Fab.) (and *P. bicyttarella* sp. n.) in having a black ground-colour, a rather distinct temporal furrow, no impressed line on the ventral half of the clypeus, and a rather larger size. So far as males have been available, all have the same type of genitalia (fig. 16c). In the present study this assemblage is divided into three species. Most of the small dark forms placed by Bequaert under the var. *parvula* (Fab.) seem to form a species recognisable by its small size, short 1st abdominal tergite (fig. 14a) and usually black clypeus. In British Guiana these forms are never found in the same nests as ordinary *P. occidentalis*, and in other parts of S. America what seem to be analogous forms are easily recognisable. In C. America, but also extending to Peru, occurs the so-called var. *diquetana* R. du Buyss., which Bequaert did not separate from his var. *parvula*. It can be distinguished, however, by its larger size, more extensive pale markings and much narrower 1st abdominal tergite. Overlapping the ranges of both these species, occur various forms of the true *P. occidentalis* (Oliv.). In the more northern parts of its range it has been possible to define a series of geographical subspecies whose ranges hardly overlap. This has not so far been possible with all the forms in the more southern part of the range. The study of nest-populations and field observations may well settle these difficulties in the future. The characters of the three species here dealt with are shown in Table 40, in which all forms of each species are amalgamated.

³¹ This specimen might well belong to *P. bicyttarella*, and it comes from a part of Brazil not very remote from the interior plateau of British Guiana. More specimens would be required to make a certain determination.

TABLE 39.

Species	No. measured	OOL : POL ratio	Hind-wing ratio	Eye/tempora ratio	Length of fore-wing (mm.)	Number of hamuli
<i>P. nigratella</i> R. du Buyss.	10	2.71 ± .35	2.95 ± .16	1.58 ± .26	8.60 ± .39	8.10 ± .32
<i>P. fastidiosuscula</i> Sauss.	16	2.78 ± .29	3.31 ± .25	1.24 ± .30	8.84 ± .49	7.31 ± .60
<i>P. cavilleyi</i> Moeb.	20	3.55 ± .45	2.44 ± .25	1.31 ± .11	9.28 ± .68	7.45 ± .60
<i>P. nidulatrix</i> Beq.	13	3.17 ± .40	2.75 ± .30	1.10 ± .05	8.00 ± .54	7.77 ± .83
<i>P. bicytharella</i> Rich.	20	2.56 ± .31	2.57 ± .25	1.70 ± .14	6.80 ± .26	6.83 ± .18
<i>P. biatriata</i> (Fab.)	20	2.54 ± .25	3.07 ± .35	1.77 ± .18	6.37 ± .24	6.25 ± .64
<i>P. biatriata</i> pale var.	11	2.48 ± .15	3.11 ± .39	1.68 ± .10	6.27 ± .26	6.55 ± .52
<i>P. occidentalis</i> (Oliv.)	30	2.12 ± .22	2.95 ± .27	1.73 ± .26	7.70 ± .38	6.99 ± .68

TABLE 40.

Species	No. studied	OOL : POL ratio	Hind-wing ratio	Eye/tempora ratio	Length tergite 1 (mm.)	Width tergite 1 (mm.)	Tergite 1 ratio	Length fore-wing (mm.)	No. of hamuli
<i>P. parvula</i> (Fab.)	77	2.71 ± .26	2.96 ± .34	1.57 ± .25	1.43 ± .08	.81 ± .05	.567 ± .039	6.94 ± .35	6.84 ± .66
<i>P. dipetana</i> R. du Buyss.	41	2.66 ± .43	3.13 ± .36	1.31 ± .13	1.64 ± .11	.72 ± .09	.439 ± .012	7.57 ± .60	7.17 ± .67
<i>P. occidentalis</i> (Oliv.)	174	2.39 ± .28	2.99 ± .35	1.51 ± .23	1.58 ± .10	.83 ± .08	.556 ± .049	7.47 ± .53	7.09 ± .69

* Some of the characters were not measured in every specimen. The numbers, however, can be found in the tables under each separate species.

TABLE 41.

Biometrical characters of *Polybia parvula* (Fab.)

Material	No. studied	OOL : POL ratio	Hind-wing ratio	Eye/tempora ratio	Length tergite 1 (mm.)	Width tergite 1 (mm.)	Tergite 1 ratio	Length fore-wing (mm.)	No. of hamuli
British Guiana, nest 85.	24	2.79 ± .26	2.64 ± .34	1.68 ± .15	1.37 ± .06	.80 ± .05	.582 ± .04	6.81 ± .32	7.00 ± .51
British Guiana, nest 205.	20	2.64 ± .20	3.11 ± .31	1.53 ± .12	1.41 ± .07	.80 ± .06	.589 ± .02	6.83 ± .37	6.95 ± .61
British Guiana, two nests, New River	20	2.77 ± .28	3.07 ± .21	1.53 ± .12	1.40 ± .05	.84 ± .04	.584 ± .02	7.08 ± .26	6.25 ± .72
All British Guiana spec.	64	2.73 ± .26	2.92 ± .34	1.59 ± .26	1.40 ± .05	.84 ± .05	.579 ± .03	6.90 ± .35	6.75 ± .67
Subsp. <i>hecula</i> Rich.	13	2.56 ± .26	3.13 ± .23	1.44 ± .16	1.56 ± .08	.79 ± .06	.506 ± .03	7.12 ± .44	6.77 ± .44
W. Ecuador, Mindo	3	2.87	2.72	1.45	1.43	.97	.652	8.17	7.67

3. *Polybia parvula* (Fab.).*Polistes parvula* Fabricius [1805].*Polybia occidentalis* (Olivier) var. *parvula* Bequaert, 1944.

This species was described from "S. America," apparently from a very dark form such as is common in British Guiana. This form is here regarded as typical.

Female. Black; mandibles black (61)³² or with a small pale spot (46); clypeus black (105) or with 2 small ventral spots (2); inner orbits black (41) or with a small pale ventral spot (66); pronotal fovea with a small pale dot (21) or black (86); posterior margin of pronotum with a narrow incomplete pale band (104) or nearly black (3); mesopleuron with a narrow central stripe to near the punctiform fovea (86) or blade (21); scutellum black (106) or with a pale dot on each side (1); postscutellum black (92), or with pale lateral dots (1), or with a very narrow anterior band (14); propodeum black with the valves pale (105), or with pale ventral spots as well (2); abdomen usually with lateral spots at the end of tergite 1 and narrow bands at the end of sternites 2-3 (87), but sometimes (18) with more bands (up to bands on tergites 1-4 and sternites 2-4) or all black (2); tegulae blackish-brown; wings hyaline with a dark mark in the radial cell; antenna with some orange suffusion beneath the scape and the proximal part of the flagellum. Clypeus usually ventrally more shining and punctured than in *P. occidentalis* (Oliv.). Biometrical characters, see Table 41. *Male* not seen.

Biological characters:—Cells 2.0 mm. diameter, 4.0 mm. deep, cocoons moderately projecting. Castes little differentiated, no intermediates seen, queens forming 16.5 per cent. of the colony. Initial colonies apparently 3-4 combs and 300-600 cells.

Specimens examined:—BRITISH GUIANA: New River, 750 ft., 1.iii.1938, nest 6, 57 ♀ (*C. A. Hudson*), 15-25.ii.1938, 1 ♀, 3.ii.1938, nest 3, 27 ♀, 26-27.iii.1938, 2 ♀; Potaro R., Kaieteur Savannah, 5.ix.1937, nest 205, 4 ♀ (*Richards and Smart*); Mazaruni Station, clearing, 23.viii.1937, nest 85, 7 ♀ (*Richards and Smart*), in colony house, 14.viii.1937, 1 ♀; Demerara R., Canister Falls, xi.1919, 1 ♀ (*A. A. Abrahams*); no precise locality, ♀ (*Rodway*), ♀ (*P. Cameron coll.*). VENEZUELA: Las Adjuntas, 959 m., 28.vi. and 4.vii.1926, 2 ♀ (*H. E. Box*). BRAZIL: Manicore, 1 ♀ (*B. Piffard*); Pará, 1 ♀; Ega, 2 ♀.

Long series of wasps from four nests of this form were available for study and were, on the whole, very uniform. In nest 85 the hind-wing ratio was unusually low (differing significantly from the means of the other nests). The meaning of this is uncertain.

EXPLANATION TO TABLE 39.

Ratios, etc., of seven species of *Polybia* in the group of *P. occidentalis* (Oliv.). The means are in each case followed by the standard deviations. The numbers measured apply to specimens used to determine the ratios; the data for wing-length and number of hamuli are based on more specimens in the following species: *P. bicyttarella* Rich. (57, British Guiana); *P. bistriata* (Fab.) (148, British Guiana); *P. occidentalis* (Oliv.) (288, British Guiana, W. of Essequibo R.). The series of *P. fastidiosuscula* Sauss. includes the typical form and the varieties *sampaioi* Ducke and *buyssoni* R. von Iher., which do not seem to differ from one another except in colour.

³² The figures in brackets give the frequencies of the various pale markings in the 107 females tabulated.

Polybia parvula (Fab.) subsp. **hecuba** subsp. n.

Female. Black; mandibles black (6) or with a small pale mark (7); clypeus black (6), with traces of yellow spots (2), or with small yellow ventral spots (4) or with a narrow, U-shaped mark (1); inner orbits with a pale ventral spot (13); pronotal fovea black (6) or with a pale dot (7); posterior margin with a narrow incomplete pale band (12) or nearly black (1), mesopleuron black (2), or with a yellow dot (2), or with a narrow central stripe to near the punctiform fovea (9); scutellum black (6), or with pale dots (2) or more or less large spots (5) on each side; postscutellum black (3), or with lateral pale dots (2), or with a very narrow pale anterior band (8); propodeum black with the valves pale (3), or with small pale ventral spots (3), or with spots extending for most of its length (6); abdomen usually (8) with pale posterior bands on tergites and sternites 1-4 or 1-5, less commonly (5) with fewer bands, down to tergites and sternites 1-3 only; tegulae dark brown (12) or with a small yellow dot (1); wings hyaline, with a dark mark in the radial cell; proximal part of antennae paler beneath. Biometrical characters, see Table 41. *Male* not seen.

Type ♀, BRAZIL: Theresopolis. Paratypes, BRAZIL: Theresopolis, ♀; Sta. Catherina, Humboldt, x.1918, ♀ (*W. Ehrhardt*); Rio de Janeiro, Corcovado, 23.v.1912, ♀ (*G. E. Bryant*). PARAGUAY: Pto. Bertoni, i, ♀ (*A. de W. Bertoni*, det. *P. occidentalis* var. *pygmaea*); Parana, Castro, ♀ (*E. D. Jones*). Also, in my collection, BRAZIL: Rio de Janeiro, Gavea, 22.viii.1923, 2 ♀ (*W. S. Bristowe*); São Paulo, Campos, 18.vii.1923, 3 ♀ (*W. S. Bristowe*); no precise locality, 1923, 2 ♀ (*W. S. Bristowe*).

This subspecies differs from what has been described as the typical form in the greater extension of the yellow markings, especially on the clypeus, propodeum and abdomen. It also has the 1st tergite considerably longer, compared with its posterior width.

Var. *ruficeps* Schrottky, 1902.

This form belongs structurally to *P. parvula* (Fab.) but differs markedly in colour, most of the dorsal surface of the head being reddish with the pale markings otherwise more or less like those of the subsp. *hecuba*. The distribution appears to coincide with the more southern part of the range of that subspecies, and the status of the form is doubtful.

Specimens examined:—BRAZIL: Sta. Catharina, ♀ (*P. Cameron* coll.). ARGENTINA: Santiago del Estero, R. Salado, near Icaño, 1902, 2 ♀ (*E. R. Wagner*).

Two other forms which probably belong to *P. parvula* have been seen. Three females from W. Ecuador: Mindo, in my collection, are entirely black except for narrow bands on tergites 1-2. Biometrically (Table 41), they are unusually distinct, and field study might show this to be an undescribed species. In the British Museum collection is a female, Costa Rica (*Patten*), which is much more yellow marked than any of the others, the scutellum, postscutellum and most of the disc of propodeum being yellow (as in *P. occidentalis* subsp. *spilonota* Cam.).

4. *Polybia diguetana* R. du Buysson, 1905.

Polybia occidentalis var. *digueta* R. du Buysson, 1905.

Polybia occidentalis var. *parvula* Bequaert, 1944 (in part).

The study of the Mexican species of the *P. occidentalis* group was very instructive. It was possible, first, to separate out a dark slender form with

very little yellow on the clypeus and a 1st tergite ratio of about 0.45. This agrees pretty well with the description of var. *diguetana* R. du Buyss. The remaining specimens which had variable but more extensive yellow markings were found to be bimodal in the distribution of the ratio (see Table 42). It

TABLE 42.

Frequencies of the 1st tergite ratio in Mexican "*P. occidentalis*."

Value of ratio	<i>diguetana</i>	Series from N. Yucatan	Other Mexican specimens	All Mexican specimens
·400-·429	3	0	0	3
·430-·459	8	0	5	13
·460-·489	8	0	6	14
·490-·519	0	0	1	1
·520-·549	0	2	1	3
·550-·579	0	4	2	6
·580-·609	0	5	4	9
·610-·639	0	9	1	10
No. specimens	19	20	20	59
Mean	·452	·595		

will be seen that there are two types of wasp, one with broader 1st tergite, the ratio being similar to that of *P. occidentalis* elsewhere, and one with a narrower 1st tergite and, on the average, a darker clypeus. This last form seems to be a distinct species which may be called *P. diguetana* R. du Buyss. It would be very desirable to supplement these conclusions by the study of nest-populations and by investigations of their biology.

Female. Black; mandibles black (9) or with small pale spot (169); clypeus black (3), or with small ventral spots (2), or with a narrow, sometimes interrupted, pale ventral margin (70), or with a moderately broad ventral U-shaped mark (103); inner orbits with no, or almost no pale spot (9) or with small to moderate pale spots below (169), one specimen also with small pale spots below the antennal sockets; pronotum with a small pale dot at the fovea (107) or no dot (71), posterior margin black (2), or with a feeble pale band (69) or with a distinct pale band (107); proepisternum with some pale marks in 5 specimens; mesopleuron black (88) or with a more or less distinct pale stripe to the punctiform fovea (90); scutellum black (75), or with pale lateral spots (80), or with spots joined, or nearly (23); postscutellum black (98), or anterior eighth pale (2), or anterior quarter to half pale (78); propodeum black (71), or 2 small ventral spots (12), or a single large yellow spot, more or less divided below (34), or a large spot not divided below (61), valves always more or less pale; abdomen black (62), or banded (usually on tergites and sternites 1-4) (116), in the banded forms the yellow of tergite 1 usually, or tergite 2 rarely, extends forwards to the spiracles; tegulae brown (140), or with a small yellow posterior spot (33), or with a large spot (5); wings hyaline, with a dark mark in the radial cell; in about two-thirds of the specimens the markings are pale whitish-yellow rather than bright lemon-yellow; clypeus often more shining with more punctures below than in *P. occidentalis*; pronotal keel often rather stronger; 1st tergite ratio 0.400-0.507 (C. America), 0.333-0.390 (Peru).

Male. Pale markings bright yellow and usually like those of the more maculated females; fore coxae beneath, and points of mesosternum, yellow; genitalia (fig. 15) as in *P. occidentalis*, end of aedeagus rounded.

Specimens examined:—MEXICO: Guerrero, 65 ♀, 2 ♂ (localities between 1000 and 7000 ft.); Vera Cruz, 36 ♀, 1 ♂; Tabasco, 20 ♀; Morelos, 1 ♀; Oaxaca, 3 ♀; Tamaulipas, 1 ♀; State uncertain, 5 ♀. GUATEMALA: Capetillo, 1 ♀; S. Geronimo, 11 ♀. BRITISH HONDURAS: Belize, 9 ♀; Stann Creek Valley, 16.ix.1933, 1 ♀ (*R. S. Pelly*); R. Grande, viii.1935, 1 ♂ (*J. J. White*). NICARAGUA: San Marios, 1 ♀. COSTA RICA: Igarazu, 1 ♀; Cache, 17 ♀. PERU: Oxapampa, 1600 m., 1940, 6 ♀ (*Weyrauch*).

The three females from Oaxaca are small, slender and nearly entirely black; they agree closely with the original description which was of specimens from this area. The females from Costa Rica have rather extensive yellow markings, and the 1st tergite ratio is a little large, though well below the average for *P. occidentalis* (Oliv.). The specimens from Peru are unusually slender, the markings are yellow (not whitish) and the abdomen has five bands; it is probably best to regard them, for the present, as a form of the present species. The biometrical characters of these forms are given in Table 43.

The only biological information about *P. diguetana* is R. du Buysson's remark in the original description (1905a), that the nest resembles that of *P. occidentalis* (Oliv.).

5. *Polybia occidentalis* (Oliv.).

(a) Subsp. *nausicaa* subsp. n.

This is the form inhabiting Mexico, Guatemala and Honduras. It probably overlaps with the subsp. *spilonota* Cam. in the south. It differs, on the average, from what is here called the typical form in having the yellow ventral margin of the clypeus usually interrupted below, the outer orbits always black, the band at the posterior margin of the pronotum narrower, the scutellum often black, and the yellow, if present, usually in the form of lateral spots, the propodeum in two-thirds of the specimens with a very large yellow spot divided below, 1st abdominal tergite longer and broader.

Female. Black; mandibles with a small pale spot (122) or black (3); clypeus with a more or less broad ventral U-mark (8), or with the U centrally interrupted (106), or with the two ventral pale spots (8) or black (3); inner orbits with a pale ventral spot (117) or black (8); one specimen with a small yellow dot beneath the malar space; pronotum with a yellow dot at the fovea (22) or none (103), posterior margin with a narrow pale band (106) or the band restricted to the centre (19); mesopleuron with a central stripe to a little below the punctiform fovea (111), or the stripe ending at the fovea (6), or black (8); scutellum nearly all yellow (1), with 2 large yellow spots (5), or 2 small spots (4), or with about the anterior fifth yellow (20), or with this narrow band interrupted (1), or black (94); postscutellum nearly all yellow (1), or one-third to one-half yellow (58), or one-fifth yellow (58), or 2 narrow yellow spots (4), or black (4); propodeum with the valves pale, and with a large yellow spot divided below (80), or with 2 moderate (36) or small ventral (7) spots, or black (2); abdomen with bands on tergites and sternites 1-5 (116), band on tergite 1 more or less wide, rarely band on sternite 5 absent (6) or on tergite 5 and sternites 3-5 absent (3); tegulae brown; antennae with segments 1-2 more or less yellow beneath and flagellum beneath orange-tinged; wings hyaline, with a dark mark in the radial cell; biometrical characters given in Table 44. In about half the specimens the yellow is rather whitish.

Male. Like the yellower females but with the clypeus entirely yellow or with a large dorsal disc black; spot on inner orbits larger, outer orbits also with the lower two-thirds yellow; pronotal band broader; fore and mid coxae, spot at articulation of femur and

TABLE 43.
Biometrical characters of the forms of *Polybia diguetiana* R. du Buysson.

Material	No. studied	OOL: POL ratio	Hind-wing ratio	Eye/tempore ratio	Length tergite 1 (mm.)	Width tergite 1 (mm.)	Tergite 1 ratio	Length fore-wing (mm.)	No. of hamuli
Spec. from Oaxaca	3	2.70	2.77	1.15	1.36	.60	.435	9.0	8.33
Mexican, clypeus dark	20*	2.69 ± .95	2.10 ± .41	1.97 ± .00	1.07 ± .09	.77 ± .04	.433 ± .03	7.53 ± .38	7.15 ± .49
Mexican, clypeus paler	13	2.67 ± .23	2.19 ± .41	1.87 ± .11	1.07 ± .03	.76 ± .06	.401 ± .03	7.50 ± .43	7.08 ± .60
All Mexican spec.	35	2.67 ± .43	2.15 ± .36	1.90 ± .12	1.08 ± .13	.75 ± .06	.424 ± .03	7.46 ± .50	7.33 ± .65
Costa Rica	10	2.68 ± .24	2.11 ± .36	1.63 ± .05	1.03 ± .03	.77 ± .06	.394 ± .03	7.45 ± .38	7.70 ± .68
Peru	6	2.59 ± .24	2.11 ± .36	1.44 ± .13	1.60 ± .09	.68 ± .03	.366 ± .03	7.17 ± .52	6.83 ± .75

* In one of these specimens the abdominal characters were not measured.

TABLE 44.
Biometrical characters of the forms of *Polybia occidentalis* (Olivier).

Material	No. studied	OOL: POL ratio	Hind-wing ratio	Eye/tempore ratio	Length tergite 1 (mm.)	Width tergite 1 (mm.)	Tergite 1 ratio	Length fore-wing (mm.)	No. of hamuli
Ssp. <i>nauseosa</i> , N. Yucatan	20	2.39 ± .23	2.02 ± .22	1.39 ± .09	1.50 ± .08	.95 ± .06	.505 ± .03	7.25 ± .33	7.25 ± .55
Ssp. <i>nauseosa</i> , rest of Mexico	8	2.55 ± .25	2.08 ± .29	1.44 ± .11	1.63 ± .07	.94 ± .04	.580 ± .03	7.75 ± .33	8.00
All of ssp. <i>nauseosa</i>	28	2.43 ± .24	2.04 ± .24	1.38 ± .12	1.60 ± .08	.94 ± .06	.591 ± .03	7.49 ± .39	7.44 ± .53
Ssp. <i>cincta</i> , British Guiana	10	2.40 ± .19	2.04 ± .26	1.41 ± .10	1.54 ± .06	.86 ± .04	.551 ± .03	6.85 ± .24	6.90 ± .57
Ssp. <i>cincta</i> , Trinidad	10	2.52 ± .21	2.05 ± .26	1.39 ± .16	1.40 ± .05	.70 ± .04	.565 ± .03	6.45 ± .37	6.60 ± .52
All of ssp. <i>cincta</i>	20	2.56 ± .23	2.05 ± .26	1.40 ± .17	1.47 ± .13	.82 ± .04	.558 ± .03	6.05 ± .41	6.75 ± .58
Ssp. <i>platycephala</i> , Marshall and R. Caroline	13	2.33 ± .25	2.05 ± .27	1.77 ± .26	1.64 ± .10	.80 ± .05	.488 ± .03	7.65 ± .48	6.77 ± .44
Ssp. <i>platycephala</i> , Mazatlan	30	2.12 ± .22	2.05 ± .27	1.53 ± .08	1.61 ± .08	.82 ± .09	.403 ± .04	7.70 ± .38	7.00 ± .66
All of ssp. <i>platycephala</i>	43	2.15 ± .24	2.05 ± .27	1.54 ± .08	1.63 ± .10	.81 ± .08	.401 ± .04	7.69 ± .45	6.83 ± .61
Ssp. <i>occidentalis</i> , Kinetour	20	2.53 ± .25	2.58 ± .27	1.43 ± .17	1.63 ± .08	.91 ± .06	.591 ± .03	7.60 ± .23	7.07 ± .63
Ssp. <i>occidentalis</i> , Minas	12	2.48 ± .22	2.85 ± .28	1.43 ± .19	1.57 ± .09	.93 ± .06	.597 ± .03	7.38 ± .28	6.83 ± .51
Ssp. <i>occidentalis</i> , S. Brazil, Argentina	21	2.30 ± .21	2.38 ± .39	1.39 ± .15	1.54 ± .10	.90 ± .07	.583 ± .04	7.41 ± .33	7.33 ± .73
All of ssp. <i>occidentalis</i> , var. <i>albopicta</i>	10	2.45 ± .25	2.92 ± .45	1.49 ± .10	1.61 ± .08	.90 ± .08	.561 ± .04	7.60 ± .35	7.39 ± .67
Ssp. <i>occidentalis</i> , var. <i>albopicta</i>	63	2.45 ± .25	2.92 ± .45	1.44 ± .15	1.56 ± .08	.91 ± .05	.579 ± .03	7.80 ± .42	7.59 ± .69
Var. <i>scutellaris</i>	20	2.47 ± .27	2.12 ± .26	1.54 ± .31	1.58 ± .10	.90 ± .06	.569 ± .05	7.90 ± .47	7.30 ± .80

tibia, anterior side of fore tibia, proximal part of tarsi, pale; abdomen with bands on tergites 1-5 or 1-6, and on sternites 1-5.

Type ♀, MEXICO: N. Yucatan (*Gaumer*). Allotype ♂, MEXICO: Tabasco, Teapa, Feb. (*H. H. Smith*). Paratypes, MEXICO: Guerrero, localities from 1000 to 4600 ft., 62 ♀; Jalisco, 4 ♀; Vera Cruz, 2 ♀; Tabasco, 2 ♀; Yucatan, 51 ♀; Guatemala, 2 ♀; Honduras, 1 ♀; one further male, MEXICO: Guerrero, Chilpancingo, 4000 ft., Sept. (*H. H. Smith*).

(b) Subsp. *spilonota* Cameron.

Polybia spilonota Cameron, 1904 (Nicaragua).

Polybia fastidiosuscula var. *nigriceps* Zavattari, 1906 (syn. n.).

This form inhabits the region from Costa Rica to Colombia and eastern Ecuador. It differs from what is here called the typical form in having the scutellum and postscutellum entirely yellow, often with an orange tinge; there is also more yellow on the propodeum.

Female. Black; mandibles with a small pale spot (35) or black (6); clypeus with a very wide U-shaped ventral mark (23), or with a normal U (11), or with small ventral spots (4), or almost black (3); inner orbits with a pale spot (38) or almost none (3); outer orbits with a small spot at the bottom (4) or black (37); pronotum with a pale dot at the fovea (5) or none (36), posterior margin with pale band widened at sides (24), or band narrow (11), or band only present near centre (6); mesonotum with a U-shaped yellow mark (9), or narrow yellow lines (1), or black (31); mesopleuron with a central stripe to the punctiform fovea (20), or to a little below the fovea (20), or with a disconnected yellow spot below (1); scutellum and postscutellum entirely yellow (41); propodeum with the valves pale and a large yellow spot which may be undivided (19) or more or less divided below (22); abdomen with bands on tergites 1-5 (35) or tergites 1-4 (6), that on tergite 1 broad, and on sternites 1-4 (41); tegulae brown (40) or with a large yellow spot (1). No specimens measured, but characters near those of subsp. *nausicaa*.

Male. Like the female, but clypeus yellow with a narrow black central stripe; outer orbits narrowly yellow, inner orbits more extensively yellow; preepisternum, all coxae and mesosternum, yellow marked.

Specimens examined:—Type ♀, NICARAGUA, San Marcos (*Cameron* coll.); also type ♀ of *P. fastidiosuscula* var. *nigriceps* Zavattari (kindly sent by Prof. Arcangeli from Turin); ECUADOR: Vines; further COSTA RICA, 6 ♀; NICARAGUA, 10 ♀, 2 ♂; PANAMA, 21 ♀; COLOMBIA (Lake Sapatoza region), 1 ♀; also one old specimen labelled "Mex."

(c) Subsp. *cincta* (Prov.).

Eumenes cinctus Provancher, 1888 (Trinidad).

This subspecies inhabits Tobago, Trinidad, the coastlands of British Guiana. It differs from what is here called the typical form in being markedly smaller, with the POL: OOL ratio somewhat larger, and the yellow markings of the pronotum more extensive.

Female. Black; mandibles with a small pale spot (89); clypeus with a large U-shaped ventral yellow mark, only failing to reach dorsal end of sides in 2 spec.; inner orbit with a spot to or, rarely, nearly to bottom of ocular sinus; usually a minute yellow spot on gena beneath mandibular articulation (except mainland forms); pronotum with a considerable yellow area around the fovea (less in mainland forms), posteriorly with a broad yellow

band which is considerably widened at sides (less so in British Guiana); mesopleuron with a central yellow stripe to, or nearly to, the punctiform fovea; scutellum and post-scutellum yellow except for an obtuse triangular, posterior, black mark; propodeum with valves pale and a large yellow spot divided below; abdomen with bands on tergites and sternites 1-5, those on tergites 1-2 rather broad, but only in 2 specimens extending forwards to the spiracles; tegulae brown with a very small posterior yellow spot or (on mainland) brown; antennae more or less pale beneath. For biometrical characters, see Table 44.

Male. Like the female, but in the one specimen seen pronotal band narrow; clypeus yellow except for a small dorsal spot; outer orbits yellow; proepisternum, coxae and mesosternum, yellow marked; tibiae and tarsi with some pale markings.

Specimens examined: TOBAGO, 23 ♀. TRINIDAD, 48 ♀. BRITISH GUIANA: Georgetown, Botanic Gardens, 12 ♀, 1 ♂, viii.1929 (*Oxford Univ. Exped.*), 2 ♀, viii.1937 (*Richards and Smart*); R. Berbice, 1 ♀ (*Rev. J. Aiken*); no precise locality, 2 ♀ (*Rodway, Bartlett*). Also one female labelled "Barbadoes," but this is almost certainly incorrect.

(d) Subsp. *grenadensis* subsp. n.

This subspecies inhabits the islands of Grenada and Balthazar (Windward Islands). It is a small form, resembling the subsp. *cincta* (Prov.), but more extensively yellow marked. No detailed biometrical study was made.

Female. Colour-pattern as in the subsp. *cincta* (Prov.) except in the following particulars: clypeus yellow with only the disc black; yellow spot on the inner orbit larger; yellow of the pronotum more extensive, the broad posterior band almost meeting the yellow area round the fovea; the yellow band of tergite 2 extending forwards along the sides half-way to the anterior margin. Length of fore-wing 6.0-7.0, mean 6.65 mm.; hamuli 7-8, mean 7.17, except for one specimen (Balthazar) in which the right wing had 11, and the left wing 10 hamuli, these numbers being outside the range for all other forms of *P. occidentalis* (Oliv.).

Male not seen.

Type ♀, GRENADA: St. George, 6.x.1937 (*Richards*). Paratypes, GRENADA: St. George, 6.x.1937, 3 ♀ (*Richards*); St. George, 2.viii.1929, 2 ♀ (*Oxford Univ. Exped.*); 1902, 1 ♀. Balthazar: Windward side, 5 ♀ (*H. H. Smith*). West Indies, 1 ♀.

(e) Subsp. *platycephala* subsp. n.

Inhabits the rain-forest area of British Guiana, between the coastal plain and the interior plateau, but the exact limits of its range to the east and west are unknown.

It differs from all the forms in the narrow tempora, smaller POL: OOL ratio, narrower 1st abdominal tergite; the pale markings are relatively reduced.

Female. Black; mandibles black (16) or with a small pale spot (34); clypeus with a narrow pale ventral margin; inner orbits with a pale ventral spot not reaching up to the ocular sinus; outer orbits with a small ventral dot in one specimen; pronotum with (25) or without (25) a pale dot at the fovea, posterior band moderately broad (27), narrow (16), or more or less abbreviated at the sides (7); mesopleuron with a broad central stripe to below the punctiform fovea (3), or with a narrow stripe to the fovea (35), or with a very

narrow stripe to, or nearly to, the fovea (6), or black (6); scutellum with yellow spots on the axillae (27), or with small (20) or large (3) lateral spots in addition; postscutellum black or with small spots on the axillae (18), or in addition with anterior sixth (4) or half (25) yellow, or nearly all yellow (3); propodeum black (4), or valves and round or oval ventral spots pale (19) or valves and large undivided disc yellow (27); abdomen with bands (broader on tergites 1-2) on tergites 1-5 and sternites 1-4 (22), or on tergites and sternites 1-4 (9), or on tergites and sternites 1-3 (18), or on tergites and sternites 1-2 (1); tegulae brown (33) or with a more or less large posterior yellow spot (17); legs dark; antennae nearly always with segments 1-2 paler beneath; wings hyaline, with the radial cell darker; biometrical characters given in Table 44.

Male. Colour-pattern as in female except: ventral and lateral margins of clypeus broadly yellow; inner orbits yellow to bottom of ocular sinus; small yellow spots between antennal sockets and clypeus; outer orbits yellow to near top of eye; pronotal band broader and a little produced outwards along the keel (except 1 spec.); scutellum one-third (or, in 1 spec., with separate spots), postscutellum two-thirds yellow; propodeum with a large undivided yellow spot or (1 spec.) 2 oval spots; tergites and sternites 1-5 with bands, that of tergite 1 more or less produced forwards along the sides; most of propisternum, underside of fore and mid coxae, streak beneath hind coxae, posterior spots on mesosternum, yellow; most of the fore tibia and tarsus, and central part of mid and hind tarsi, yellow; antennae with segments 1-2 yellow, other segments orange-brown beneath; tegulae brown with an outer testaceous area; as usual in the genus, clypeus with silvery pubescence and more obtuse below, tempora narrow, and 7th sternite flattened.

Biological characters:—Cells of comb 2.5-2.7 mm. in diameter, 6.0 mm. deep, cocoons projecting 3.5 mm. Queens forming, on the average, 7.0 per cent. of the colony, intermediates very rare, workers rather well differentiated though not, apparently, in colour-pattern.

Type ♀, BRITISH GUIANA: Mazaruni Station, clearing, nest 10, emerged 14.viii.1937 (*Richards and Smart*). Allotype ♂, same nest, 11.viii.1937. Paratypes, 49 ♀, tabulated above, *viz.* Mazaruni Station, clearing, flying, 1 ♀, in colony house 11 ♀, from nests 10, 26, 34, 105, 275, 301, 314—1, 5, 5, 4, 4, 1 and 3 ♀, respectively; Essequibo R., first falls, nest 1949, 10.ix.1929, 11 ♀ (*Oxford Univ. Exped.*); Courentyne R., King Frederick William IV Falls, 14-22.iii.1936, 3 ♀; 2 ♂ same nest as allotype, 1 ♂ in colony house, 12.viii.1937.

It seems strange, at first sight, that an unusually distinct subspecies should be developed in an area of rain forest which is not sharply bounded on either the coast or inland margin, each of which is inhabited by a different subspecies. Davis (1941), however, points out that approximately the same area is inhabited by a surprisingly large number of endemic trees. He puts forward the interesting hypothesis that most of the area was covered by the sea in late Tertiary or even early Quarternary times. The species must have survived at that time on the small volcanic hills (then islands) which rise at various points to about 300 m. from the peneplain. A number of small isolated islands would provide the best conditions for rapid evolution, while after the area emerged from the sea there would have been an invasion of the land joining up the volcanic hills. Davis' paper should be consulted for more detailed information. Whether *Polybia bicyttarella* Rich. (p. 134) can be regarded as a parallel case is uncertain, since it has a wider range inland, reaching the Kaieteur Savannah. Presumably, the establishment of subsp. *cincta* (Prov.) on the coastal plain must have been due to a still later invasion, probably from the direction of Trinidad.

(f) Subsp. *flavifrons* Smith, 1857.*Polybia flavifrons* Smith, 1857.

This form was described from Ecuador, and all specimens seen have come from Ecuador and Peru. Bequaert (1944 : 286) gives it a much wider range, but I feel confident that he includes under the same name specimens such as are here referred to the var. *albopicta* Smith (p. 146). The subsp. *flavifrons* is very extensively yellow marked and, in particular, has yellow side-lines on the mesonotum and spots on the metapleuron which have not been seen in any other form. The biometrical characters have not been studied but seem to be very close to those of the typical form.

Female. Black; mandibles with a small yellow spot (27) or none (1); clypeus yellow except dorso-lateral sutures (7), or with a small black spot (1), or with a larger black disc (20); frontal region with small black spots in the antennal scrobes (16) or these spots nearly obsolete (12), and with a black bilobed spot enclosing the ocelli (7) or the black bilobed spot much larger and enclosing 3 anterior yellow dots (5) or an anterior yellow trident (16); outer orbits broadly yellow (28); yellow of occiput joined to that of both inner and outer orbits (8), or to that of inner orbits only (9, including type), or to that of outer orbits only (5), or yellow of both orbits separate (6); pronotum with a pale spot at fovea and a narrow pale anterior margin, posterior margin with a moderately broad band which is somewhat produced along the keel except in 1 spec.; pronotum with lateral yellow lines next the tegula and a pair of discal lines which are rectangularly joined in front of the scutellum (16) or just separate here (12); mesopleuron with a yellow central stripe to a little below the punctiform fovea; scutellum yellow except for narrow central and posterior lines (7) or central quarter black (21); postscutellum yellow with a narrow (7) or rather broader (21) black posterior line; propodeum with valves and 2 large oval spots yellow; metapleuron with a dorsal and ventral yellow spot; propisternum with a small yellow spot (7) or black (21); fore coxae mainly yellow, mid coxae with a yellow spot in 1 specimen; mesosternum with moderate yellow spots (1), or the posterior processes yellow (10) or black (17); legs with distal part of femora yellow, and tibiae and tarsi mainly brown (6) or legs darker (22); abdomen with yellow bands on tergites and sternites 1-5, those of tergites 1-2 produced forwards to the spiracles; tegulae yellow with a large outer brown spot; antennae more or less pale beneath, and sometimes partly pale above the first 3 segments; length of fore-wing 6.0-7.5, mean 6.82 mm.; hamuli 6-9, mean 7.96.

Male. Pattern as in one of the yellower females.

Specimens examined:—ECUADOR: Guayaquil, ♀ type (B.M.); Guayaquil, 1 ♀; South-west Ecuador, 4 ♀ (*R. Wright-Barker*); no precise locality, 1 ♀ (*G. Hammond*). PERU: Valle Chicana, 11 ♀, 1 ♂ (*Weyrauch*); near Chichlayo, Olmos, iii. 1947, 10 ♀ (*Weyrauch*). The 21 females from Peru include all the dark specimens tabulated above. F. Smith wrongly supposed Guayaquil to be in Venezuela.

Polybia saussurei Holmgren, 1868, appears from the description and from the statement of Bequaert (1944 : 288), who saw the type, to be very similar to the subsp. *flavifrons* Smith. Nevertheless, as it was described from Mexico (California and Puna), the type seems to require further study.

(g) Subsp. *occidentalis* (Olivier).*Vespa occidentalis* Olivier, 1791.

Both *Vespa occidentalis* and *Vespa pygmaea* Fabricius, 1793, were described from Cayenne and were clearly based on one of the forms of the present species.

Unfortunately, no specimens from this area have been available for study, and the descriptions are insufficiently detailed to be sure which subspecies was involved. It is proposed, temporarily, to use the name *occidentalis* for the form of the species which is found in the greater part of Brazil, extending in the north-west to the interior of British Guiana and to Venezuela, and in the south to northern Argentina. The southern specimens tend to be darker than the north-western ones, with the yellow clypeal markings more often divided, the pronotal band rather narrower and the yellow spots on the propodeum smaller.

Female. Black; mandibles with a small pale spot (69) or black (1); clypeus with 2 ventral spots, sometimes just joined (31), or a large ventral U-shaped mark (16), or yellow with a large dorsal disc (about two-thirds) black (20); inner orbits with a small pale spot (1), or a spot to the bottom (54) or centre (15) of the ocular sinus; small yellow spots below the antennal sockets (16) or none (54), small yellow dots above the antennae (6) or none (64); outer orbits black (29), or with a minute ventral yellow dot (9) or dorsal and ventral dots (2), or a more or less interrupted (14) or complete yellow band (16); pronotum with a yellow dot at the fovea (26) or none (44), with a band along the posterior which may be rather broad and a little produced along the keel (2), or broad but not so produced (36), or rather narrow (32); mesonotum black (53) or with more or less distinct discal yellow lines (17); mesopleuron with a central yellow stripe to the punctiform fovea (58) or to well below it (12); scutellum black (1), or with 2 yellow spots (9), or with a band occupying less than half (31) or more than half (29) of the anterior part; post-scutellum anteriorly less than half yellow (37) or half or more yellow (33); propodeum with the valves pale and 2 small (8) or large oval spots (62); abdomen with bands on tergites 1-5 and sternites 1-4 yellow (35), band of tergite 1 usually wider and rarely (4) produced forwards along the sides, or tergites and sternites 1-4 (34) or tergites 1-3 and sternites 1-2 (1) with bands; tegulae brown (52), or with small posterior yellow spot (12) or a large one (6); antennae more or less extensively pale beneath; legs dark, in 1 spec., with a yellow dot on the hind coxae; biometrical characters given in Table 44.

Male. Markings as in the yellower females but fore coxae mainly yellow beneath, and mid coxae with a yellow spot.

Specimens examined:—VENEZUELA: Petare, near Caracas, 22.vi.1926, ♀ (*H. E. Box*); Las Adjuntas, 959 m., 28.vi.1926, ♀ (*H. E. Box*); no precise locality, 1 ♀. BRITISH GUIANA: Kaieteur Savannah, nest 155, 2.ix.1937, 14 ♀, 1 ♂ (*Richards and Smart*). PERU: Cojamarca, Celandin, 2600 m., 2 ♀, 3 ♂ (*Weyrauch*). BRAZIL: Amazons region, 19 ♀; Minas Geraes, 2 ♀; S. Paulo, 4 ♀; Rio de Janeiro, 3 ♀; Pernambuco, 1 ♀; no precise locality, 11 ♀. ARGENTINA: Santa Fé, 7 ♀; Entre Rios, 2 ♀, 1 ♂; Alto Parana, 1 ♀; no precise locality, 1 ♀.

The specimens from Cojamarca, Peru, are large, with the 1st tergite very strongly angled at the spiracles; the yellow pattern is somewhat peculiar, and more specimens from this region would repay study. There are also two abnormal females from Pará which are as dark as specimens of *P. parvula* (Fab.), with the clypeus black but rather resembling the present subspecies in structure. Clearly, nest populations from a number of the localities should be examined.

(h) Var. *albo* = *picta* Smith, 1857.

This form, which was described from "Brazil," appears to be made up of a selection of the yellowest specimens of the typical subspecies, though they

are not completely interconnected in the material available for study. At first sight the postpetiole seemed to be more expanded, but measurement (Table 44) showed that the 1st tergite ratio, at any rate, did not differ significantly from the subsp. *occidentalis*. Nest-populations will be required to settle the status of this form.

Female. Black; mandibles with a small yellow spot; clypeus entirely yellow (12) or with a small black discal spot (5); inner orbits to near centre of ocular sinus and outer orbits broadly yellow; area beneath, between and a little above the antennal sockets yellow; pronotum with a yellow dot at the fovea (14) or none (3), posteriorly with a moderate (16) or very broad (1) band; mesonotum on disc with interrupted U-shaped yellow mark (6), or traces of 2 yellow lines (6), or black (5); mesopleuron with a broad central stripe to well below the punctiform fovea and, in 1 spec., a disconnected yellow spot as well; scutellum and postscutellum mainly yellow with a small obtusely triangular posterior black mark; propodeum with the valves and 2 large oval marks yellow; abdomen with yellow bands on tergites 1-5 and sternites 1-4, broader on tergites 1-2 (13), or produced along sides of tergite 2 (4); tegulae with a small posterior yellow spot (2) or with a large spot to mainly yellow (15); antennae with segments 1-2 yellow beneath, flagellum more or less orange beneath; legs mainly dark; biometrical characters given in Table 44.

Male. Resembles in pattern the yellow specimens of the female.

Specimens examined:—Type ♀, BRAZIL (Swainson). VENEZUELA: Caracas Valley, Las Ruices, 24.v.1926, ♀, vii.1926, ♂ (*H. E. Box*); Arvelo, north of Petare, 22.vi.1926, 2 ♂ (*H. E. Box*). BRAZIL: Pará, 5 ♀ (*A. M. Moss*); Bahia, 3 ♀ (*Challenger Exped.*); no precise locality, 7 ♀ (one with ♀ Strepsipteron beneath the right side of tergite 4).

(i) Var. *jurua* R. von Ihering, 1904.

According to Bequaert (1944: 287), this form is found in a large area of the upper Amazon and its tributaries. How far this region overlaps the areas occupied by the typical form and by the subsp. *flavifrons* Smith seems to be uncertain. The few specimens examined seem to be structurally like the typical form but rather small; they are distinguished especially by having the greater part of tergite 2 yellow.

Female. Black; small spot mandibles, broad U-shaped ventral margin to the clypeus inner orbits to bottom of ocular sinus, centrally interrupted band of outer orbits, moderate posterior pronotal band, broad central stripe of mesopleuron to below the punctiform fovea, scutellum, anterior two-thirds of postscutellum, valves and rather large oval spots of propodeum, moderate band of tergite 1, more than half of tergite 2 (less at sides), broad bands tergites 3-5, bands sternites 1-4, yellow; tegulae brown; antennae dark, segment 1 yellowish beneath; legs dark.

Specimens examined:—BRAZIL: Amazons, R. Jurua, ♀ paratype; S. Paulo, 3 ♀. PERU: Valle Chanchomayo, 800 m., 1939, 3 ♀ (*Weyrauch*). According to Ducke (1910: 497) the var. *jurua* makes very small nests.

(j) Var. *scutellaris* (White).

Myrapetra scutellaris White, 1841.

This form provides what is the major unsolved problem in the taxonomy of this group. I feel confident that it will ultimately be shown to be a distinct

species, but the evidence is at present too contradictory for such a claim to carry enough weight.

The variety *scutellaris* is found in the area from south-east Brazil to Argentina, occurring in the same localities as the subsp. *occidentalis* (Oliv.). The colour-patterns are distinct, but the occurrence of specimens which are, at least in some respects, intermediate indicates the need for caution. Apart from its larger size, it shows no important difference in the biometrical characters studied, and careful examination has not so far revealed any others. Characteristically, var. *scutellaris* is found in very large nests, which last several years and of which the envelope is covered with spinose processes (cf. p. 51). Unfortunately, Ducke (1910: 497) claims that nests of an intermediate type inhabited by wasps with a transitional pattern have been found. This may be partly explained by Bruch's observation (1936), that the spinose processes are almost absent in young nests and are enlarged as the colony grows. The taxonomy of the group was so confused in Ducke's work that there is clearly a need for the examination of a number of nest-populations and of their nests.

Female. Black; small pale spots at the bottom of the inner orbits (13) or none (44); pronotum with a narrow, often incomplete, pale posterior margin (24) or none (33); mesopleuron with a small yellow spot or dot (7) or black (50); scutellum entirely yellow (53), or the posterior quarter to half black (4); postscutellum entirely yellow (2), or anterior two-thirds (38), anterior half (15), or about anterior quarter (2), yellow; abdomen black (38), or end of tergite 1 with small spots (3) or a pale band (8), or spots at the ends of tergites 1-2 (3), or tergite 1 with a narrow band, and tergites 2-4 with spots (5); propodeum, tegulae, antennae and legs dark; biometrical characters given in Table 44.

Male. Large U-shaped pale mark on clypeus, inner orbits nearly to bottom of ocular sinus, dorsal two-thirds of outer orbits, narrow posterior pronotal band, scutellum, anterior half of postscutellum, spot on propisternum, underside of front coxa, streak on front tibia, band on abdominal tergite 1, hardly traceable bands on other tergites, yellow.

Specimens examined:—BRAZIL: type ♀; S. Paulo, 3 ♀; Rio de Janeiro, ♀; Sta. Catharina, 7 ♀, 1 ♂; no precise locality, 1 ♀. PARAGUAY, 2 ♀. URUGUAY, 17 ♀. ARGENTINA: Alto Parana, 3 ♀; Parana delta, 4 ♀; Misiones, 7 ♀; no precise locality, 2 ♀.

KEY TO THE FORMS DEALT WITH IN THIS APPENDIX.

1. Tempora without or with only faint traces of a furrow. Clypeus usually with an impressed line on ventral third. Size smaller. Male penis valves with sides straighter distally. Ground-colour not black. 2.
- Tempora with a more or less distinct furrow. Clypeus without an impressed line. Size larger. Male penis valves distally with sides rounded (fig. 16c). Ground-colour black. 3.
2. Hind-wing ratio averaging 2.57 (range 2.15-3.08). Colour pale orange-brown without oblique pale lines behind the ocelli. Male with most of mesopleuron and mesosternum pale and sides of penis valves less convergent. British Guiana (except coast); possibly Brazilian Guiana *P. bicyttarella* Richards p. 132.
- Hind-wing ratio averaging 3.07 (range 2.49-3.90). Colour often chocolate-brown with oblique pale lines behind the ocelli, but sometimes very similar to previous species. Male with only moderate pale areas on mesopleuron and mesosternum, and sides of penis valves more convergent. Brit. Guiana, N.W. Brazil, Peru

P. bistriata (Fab.), p. 134.

3. First abdominal tergite long and relatively narrow, width/length ratio averaging 0.44. C. America, Peru *P. diguetana* du Buyss., p. 138.
- First abdominal tergite with width/length ratio averaging 0.56 4.
4. Smaller, 1st abdominal tergite shorter. Clypeus usually black (only in south-eastern subspecies are yellow markings frequent), ventrally often with more numerous punctures. Whole body normally less yellow marked *P. parvala* (Fab.) 5.
- Larger, 1st abdominal tergite longer. Clypeus almost always yellow marked, usually with a conspicuous yellow ventral margin, punctures rarely evident. Yellow markings generally more extensive
P. occidentalis (Oliv.) 7.
5. Head dorsally largely reddish. S.E. Brazil, N.E. Argentina
var. ruficeps Schrottky, p. 138.
- Head black, usually with some small pale spots 6.
6. Width/length ratio of 1st abdominal tergite averaging 0.51. Clypeus with some pale markings in half the specimens. Propodeum with obvious pale spots in 3 out of 4 specimens. Abdominal tergites usually with 4 or 5 pale bands. S.E. Brazil, Paraguay
subsp. *hecuba* Richards, p. 138.
- Width/length ratio of 1st abdominal tergite averaging 0.58. Clypeus and propodeum with pale markings in only about 2 per cent. of specimens. Abdominal tergites usually with only 1, often interrupted, band. Venezuela, Brit. Guiana, N.W. Brazil
subsp. *parvula* (Fab.), p. 137.
7. Mesonotum with yellow side-lines and often yellow discal lines. Metapleuron with dorsal and ventral yellow spots. Head extensively yellow marked. Ecuador and Peru . . . subsp. *flavifrons* Smith, p. 145.
- Mesonotum without yellow side-lines. Metapleuron black, except sometimes extreme dorsal margin 8.
8. Tempora rather narrow, eye/tempora ratio about 1.74. Pale markings not very extensively developed. Central forest area of Brit. Guiana
subsp. *platycephala* Richards, p. 143.
- Tempora broader, eye/tempora ratio about 1.3 to 1.5 9.
9. Abdominal tergite 2 at least half yellow in centre (less than this at sides). Size rather small. Outer orbits entirely yellow
var. juruana R. von Iher. p. 147.
- Abdominal tergite 2 with at most a rather narrow posterior yellow band which may be somewhat produced forwards at the sides 10.
10. Small forms with the yellow pronotal band usually widened at the sides. Trinidadian region 11.
- Larger forms with the yellow pronotal band usually less widened at the sides 12.
11. Yellow band of tergite 2 extending forwards half-way to anterior margin. Grenada and adjacent islands . . . subsp. *grenadensis* Richards, p. 143.
- Yellow band of tergite 2 extending forwards in only about 2 per cent. of the specimens. Tobago, Trinidad and coast of British Guiana
subsp. *cincta* (Prov.), p. 142.
12. Scutellum entirely, postscutellum more than half yellow. Clypeus, mesopleuron, propodeum and abdomen black, or nearly so. S.E. Brazil to Argentina *var. scutellaris* (White), p. 147.
- Scutellum and postscutellum not mainly yellow in specimens in which the other parts have such reduced yellow markings 13.
13. Scutellum and postscutellum entirely yellow, often with an orange tinge. Outer orbits with at most a small yellow spot at bottom. Nicaragua to Colombia and E. Ecuador . . . subsp. *spilonota* Cam., p. 142.

- Scutellum and postscutellum very rarely entirely yellow 14.
- 14. Yellow marks of clypeus joined in less than 7 per cent. of specimens.
Outer orbits black. Yellow pronotal band narrow. Scutellum black
in three-quarters of all specimens. Mexico and Honduras
subsp. *nausicaa* Richards, p. 140.
- Yellow marks of clypeus joined in more than half the specimens. Outer
orbits more or less distinctly yellow marked in more than half the
specimens. Yellow pronotal band broader. Scutellum nearly always
yellow marked 15.
- 15. Clypeus with at least a large dorsal black spot. Venezuela and interior
of Brit. Giana to S. Brazil and Argentina subsp. *occidentalis* (Oliv.), p. 145.
- Clypeus yellow, at most with a minute black spot. Outer orbits always
broadly yellow var. *albo-picta* Smith, p. 146.

19. APPENDIX 2.

The species of *Apoica* Lep.

A study of this genus, partly employing biometrical methods, shows that all the principal colour-forms are distinct species, one of them, *A. arborea* Sauss., particularly so. *A. pallens* (Fab.) appears to be composite, but the variation is not simply geographical, and more material, particularly series of both sexes from nests, would be necessary for a complete analysis. Males have been seen of three of the five species and they show small but significant differences in their genitalia. Besides the length of the fore-wing, from the centre of the tegula to the tip, and the number of hamuli, the following characters were measured with a screw-eyepiece micrometer: length of 1st abdominal tergite from posterior end of exit-hole of dorsal muscle to centre of posterior margin; maximum width of 1st abdominal tergite at posterior margin; ratio width of eye divided by width of tempora at level of centre of eye, seen in profile so that the base of the nearer antenna is just not visible (not measured in every specimen). Means of the characters measured are followed by the standard deviations.

The following keys will serve to separate the species.

FEMALES.

1. Antennae with flagellum more knotted beneath. Scutellum less convex, its disc less raised above the mesonotum. Postscutellum less abruptly convex, not falling so perpendicularly onto the propodeum, its bristles shorter. Fore-wings with the parastigma³³ shorter. First abdominal tergite shorter and relatively broader, with shorter pubescence. Abdominal tergites brown or blackish brown with narrow posterior pale yellow bands. First axilla of fore-wings pale yellow, much paler than the tegula. Size small *A. arborea* Sauss.
- Antennae with the flagellum less knotted beneath. Scutellum more convex, more raised above the mesonotum. Postscutellum more convex, falling perpendicularly onto the propodeum, its bristles longer. Fore-wings with parastigma longer. First abdominal tergite longer, relatively narrower posteriorly, with longer pubescence.

³³ The term *parastigma*, used by Kieffer in the BETHYLIDAE, is a convenient one to describe the part of the vein Sc + R, between where M leaves Sc + R + M and the pterostigma. This structure is of considerable importance in the classification of the Aculeates.

- Abdomen with pale bands (usually less well defined) only in some forms of *A. pallens* (Fab.). First axilla of fore-wings of same colour as tegula or rather darker 2.
2. Abdominal tergites normally pale yellow, "frosted" with short silvery pubescence; more rarely proximal part of tergites somewhat darker so that there are ill-defined pale posterior bands. Scutellum and postscutellum entirely pale yellow *A. pallens* (Fab.).
- Abdomen mainly testaceous, areas on tergites 1, 2 and 6 sometimes yellow but never "frosted." Scutellum at most with small yellow spots, postscutellum often partly yellow 3.
3. Somewhat smaller species, with thorax brown and wings paler. Tergite 6 pale yellow, postscutellum with disc yellow, mesonotum sometimes with yellow lines. Depression in which pronotal fovea lies smaller and shallower. Tempora on the average narrower *A. pallida* (Oliv.).
- Larger species, with mesonotum almost black, without traces of yellow lines, wings darker. Tergite 6 with at most posterior half, or less, yellow, postscutellum dark. Depression in which pronotal fovea lies larger and deeper. Tempora on the average broader 4.
4. Abdominal tergite 2 with about the proximal half pale yellow. Postscutellum raised into a central keel-like tubercle. *A. albimacula* (Fab.).
- Abdominal tergite 2 brown, concolorous. Postscutellum usually rounded, very rarely with traces of the tubercle *A. thoracica* R. du Buyss.

MALES.

(Not known in *A. thoracica* and *A. albimacula*).

1. Male genitalia with the cuspis (in sense of Snodgrass) almost straight; aedeagus distally narrow and parallel-sided, ventral median process conspicuous, blackened; end of paramere more pointed (figs. 17-19). Antennal flagellum considerably knotted, segment 13 twice as long as broad. Clypeal margin distinctly angular. Scutellum and postscutellum with only very inconspicuous short pubescence. Abdominal tergites with narrow, well-defined yellow bands, not frosted *A. arborea* Sauss.
- Male genitalia with the cuspis strongly curved (fig. 20); aedeagus expanded distally, ventral median process less conspicuous, not blackened; end of paramere more rounded (fig. 22). Antennal flagellum not knotted, segment 13 shorter. Scutellum and postscutellum with much longer and more numerous bristles. Abdominal tergites with at most ill-defined yellow bands, though often entirely yellowish. 2.
2. Abdomen testaceous with small yellow spots at each side of the end of the 1st tergite, not at all frosted. Clypeus with ventral margin distinctly angular. Aedeagus (fig. 21) with the distal end somewhat thickened, both in dorsal and lateral view (somewhat upturned), sides very little convergent towards the ventral median process *A. pallida* (Oliv.).
- Abdomen considerably yellow-marked to entirely yellow dorsally, usually more or less frosted. Clypeus with ventral margin more obtuse. Aedeagus gradually expanded distally and not all upturned, more narrowed towards the ventral median process *A. pallens* (Fab.) 3.
3. Aedeagus in front of ventral median process broader, at least half as broad as the less expanded distal end (fig. 23). Larger, wing-length about 16.0 mm. Ground-colour of mesonotum darker to blackish. Abdominal tergites usually with indications of paler posterior bands, surface little frosted Form A.

- . Aedeagus in front of ventral median process narrower, hardly half as broad as the more expanded distal end (fig. 24). Smaller, wing-length about 15.0 mm. Ground-colour of mesonotum paler, to pale testaceous yellow. Abdomen with tergites more uniformly pale yellow, usually well frosted. Form C.

1. *Apoica pallida* (Olivier, 1791).

Female (53 examined). Testaceous to pale reddish-brown, including tegula and 1st axilla of fore-wing; 2nd axilla and antennae (except last 3-4 segments) darker; more or less distinct pale spots at shoulders of pronotum in 26 spec.; top half of prepectus yellow, except in 3 spec.; traces of yellow lines on mesonotum in 21 spec.; scutellum with axillae more or less yellow in 3 spec., disc with spots in 8 spec., whole scutellum yellow in 1 spec.; centre of postscutellum usually yellow, entirely brown, 3 spec., entirely yellow, 1 spec.; propodeum with 2 yellow spots in 6 spec., with a large undivided yellow spot in 1 spec.; abdominal tergite 1 with small posterior spots in 8 spec., with posterior band in 6 spec.; tergite 6 usually pale yellow, less yellow to brown in 6 spec. Wings moderately brown. Fore-wing 15.75-19.25, mean 17.6 ± 0.80 mm. Hamuli 13-20, mean 16.9 ± 1.33 . Eye/tempora ratio (10 spec. measured) $0.665-0.859$, mean 0.767 ± 0.06 . Length of 1st abdominal tergite $3.38-4.32$, mean 3.75 ± 0.16 mm. Ratio width/length, 1st abdominal tergite, $0.366-0.463$, mean 0.392 ± 0.0107 .

Male (3 examined). Dark testaceous, most of the flagellar segments above and the second wing axilla darker, clypeus paler; the following marks are yellow, narrow area on occiput, narrow outer orbits, pronotum behind the keel, 4 more or less distinct lines on mesonotum, some or all of the scutellum, the postscutellum, the top half of prepectus, a spot below the mesepimeron, a spot at bottom of metapleuron, large spots on the propodeum, small spots at the end of the 1st abdominal tergite; abdomen not "frosted." Length of fore-wing 14.75-15.75, mean 15.1 mm. Hamuli 15-18, mean 16.0. Length of 1st abdominal tergite $3.53-3.55$, mean 3.54 mm. Ratio width/length 1st abdominal tergite $0.420-0.486$, mean 0.452 .

Specimens examined:—TRINIDAD: Artinola Estate Rd., 700 ft., 1937, 2 ♀ (*J. Smart*); no precise locality, 7.viii.1923, 2 ♀ (*H. A. Ballou*), 2 ♂, v.1921 (*L. E. Cheesman*). VENEZUELA: Caracas, 5 ♀; La Guaira, 20.v.1913, ♀ (*F. A. Philips*). BRITISH GUIANA: Potaro R., Kaieteur Savannah, 1-8.ix.1937, 4 ♀, Garroway Stream, 30.viii.1937, 1 ♀ (*Richards and Smart*); Mazaruni R., colony house, 16.viii.1937, ♀ (*Richards and Smart*), Hills Estate, 10.iv.1926, 2 ♀ (*L. D. Cleare, Jr.*); Demerara, 4 ♀; no precise locality, 9 ♀ (*A. W. Bartlett*); Courentyne-Amazon divide, Head Oronoque R., 1937, ♀; Oronoque and New R. Heads, 1938, ♀ (*Beddington*). SURINAM: 5 ♀ (*G. Bünsli*). BRAZIL: Prov. Pará, Santarem, vi.1935, ♀ (*G. V. Vredenburg*); Pará, 6 ♀; W. end of Parana de Buysacu, 17.i.1896, ♀ (*E. E. Austen*); Obidos, 2.ii.1896, ♀ (*E. E. Austen*); Amazons, The Narrows, 5.vi.1934, ♀ (*E. H. Squire*); Amazons, ♀ (*Trail*); no precise locality, ♂♀. EAST PERU: 2 ♀. No locality, 1 ♀.

2. *Apoica thoracica* R. du Buysson, 1906.

Female (32 examined). Dark reddish-brown, ventral part of thorax and 1st abdominal tergite somewhat paler, mesonotum and 2nd axilla of fore-wing blackish. The following markings may be pale yellow: traces of a spot on upper half of prepectus in 5 spec.; anterior half of disc of postscutellum except 4 spec. in which there is only a trace of this spot and 8 in which it is absent; propodeum with traces of spots in 1 spec., and long oval spots in 1 spec.; posterior margin of 1st abdominal tergite with small spots in 1 spec., last quarter of 6th tergite yellow in 9 spec., and posterior half in 1 spec. Wings consider-

ably darker than in *A. pallida* (Oliv.) Fore-wing 17.75–19.75, mean 18.61 ± 0.51 mm. Hamuli 15–20, mean 17.70 ± 1.55 . Eye/tempora ratio (13 spec. measured) 0.764–1.167, mean 0.950 ± 0.072 . Length of 1st abdominal tergite 3.78–4.57, mean 4.25 ± 0.17 mm. Ratio width/length 1st abdominal tergite 0.364–0.505, mean 0.405 ± 0.0261 . Male not seen.

Specimens examined :—BRITISH GUIANA : Essequibo R., Weriwera-kuru Creek, 10.x.1922, ♀ (*L. S. Hohenkirk*); Essequibo R., Moraballi Creek, 27–30.viii.1939, 2 ♀, nest 1999, 12.ix.1929, 8 ♀, Wallaba forest, 19.xi.1929, ♀ (*Oxford Univ. Exped.*); Cuyuni R., clearing, 20.xi.1929, ♀ (*Oxford Univ. Exped.*); New River, 750 ft., 18–25.ii.1938, 4 ♀, 25.ii.–15.iii.1938, ♀, 28–31.iii.1938, ♀ (*C. A. Hudson*). ECUADOR : Cuenca, ♀. BRAZIL : Prov. Pará, Guampa, vi.1935, ♀ (*G. V. Vredenburg*); 500 m. up river Madeira and 50 m. east, ♀; no precise locality, 4 ♀. PERU : Oxapampa, 1600 m., 1940, 6 ♀ (*Weyrauch*).

The specimens from British Guiana have appreciably fewer hamuli than those from Brazil, Ecuador and Peru, although their wings are almost as long. The figures are as follows : 19 ♀, British Guiana, mean wing-length 18.54 mm., mean no. of hamuli 17.1; 13 ♀, Brazil, etc., mean wing-length 18.71 mm., mean no. of hamuli 18.5.

3. *Apoica albimacula* (Fabricius [1805]).

Female (54 examined). Dark brown, mandibles and abdominal sternites 2–6 reddish; abdominal tergites 2–6 reddish-brown; narrow posterior band of abdominal tergite 1 and anterior three-fifths of tergite 2, pale yellow; tegula brown, 2nd axilla darker; wings very dark brown. Fore-wing 16.75–19.25, mean 18.12 ± 0.59 mm. Hamuli 14–19, mean 16.57 ± 1.021 . Eye/tempora ratio (10 spec. measured) 0.813–1.149, mean 0.972 ± 0.05 . Length of 1st abdominal tergite 3.32–4.10, mean 3.89 ± 0.16 mm. Ratio width/length 1st abdominal tergite 0.373–0.483, mean 0.418 ± 0.029 .

Specimens examined :—BRITISH GUIANA : Essequibo R., Moraballi Creek, 2.ix.1929, nest 1368, 52 ♀ (*Oxford Univ. Exped.*); Georgetown, Botanic Gardens, viii.1929, ♀ (*Oxford Univ. Exped.*); Kutari Sources, 10.ii.–10.iii.1936, ♀ (*G. A. Hudson*).

The fact that all but two of the specimens came from a single nest means that the diagnosis may have to be altered in the light of further material.

4. *Apoica pallens* (Fabricius [1805]).

The treatment of this species is still unsatisfactory. Two types occur in both sexes. They are connected by intermediates, and are only very partially geographically segregated. On top of this, the colour-pattern seems to be much more variable than in the other species. More nest-series, including both sexes, are needed to settle these difficulties.

The larger form, with male genitalia of type A, is the only representative in Central America and the characteristic form of Colombia. The smaller form, with male genitalia of type C, is the only representative in Trinidad and Venezuela, and one set of 31 ♀, from a nest in Brazilian Guiana, is of the same type. But in general, in British Guiana, N.W. Brazil and Peru, the two forms occur mixed, together with intermediates. One female from Paraguay seems to belong to type A.

The separation of the two types of females may be made almost complete by calculating a discriminant function (Fisher, 1936; Mather, 1943:152) based on measurements of four variables, length of fore-wing, in mm. (x_1), number of hamuli (x_2), length of 1st abdominal tergite, in mm. (x_3), and ratio of width to length of 1st abdominal tergite (x_4).

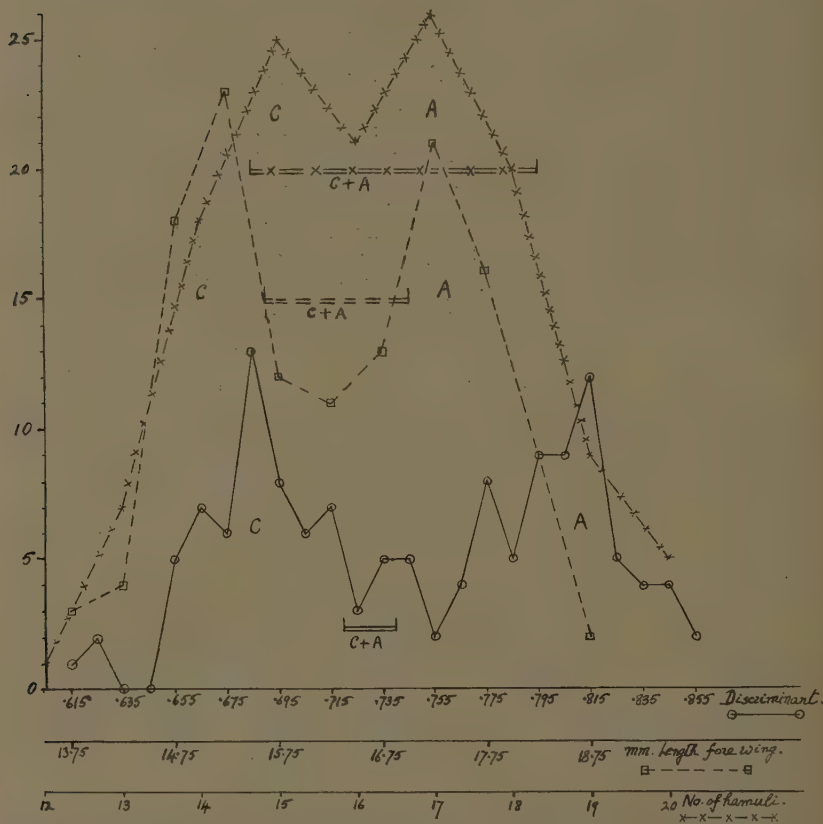


FIG. 25.—The separation of the females of the two forms (C and A) of *Apoica pallens* (Fab.), showing the small overlap in the value of the discriminant function, compared with the large overlaps in the values of length of fore-wing and number of hamuli.

The function is of the form $\lambda_1 x_1 + \lambda_2 x_2 + \lambda_3 x_3 + \lambda_4 x_4$, the values of the four λ 's being calculated from the 132 ♀ examined, so as to give the clearest separation of the two forms. The method actually employed was as follows. Thirty-seven females (Brazilian Guiana, Trinidad, Venezuela) which seemed to be pure form C, and 37 females (British Honduras, Panama, and Colombia), which seemed to be pure form A, were used to calculate preliminary values of the four constants. A discriminant function could then be used to separate

the remaining mixed series into two sets, making in all 72 ♀ of form A and 60 ♀ of form C. The definite values of the constants were then recalculated from the complete material. The four constants have the following values: $\lambda_1 = 0.037537$, $\lambda_2 = 0.007654$, $\lambda_3 = 0.008551$, $\lambda_4 = -0.045357$. The measurements of the wing-length, number of hamuli, length of 1st abdominal tergite, and the ratio width/length of the tergite, must be multiplied by the corresponding constant and added (with the last, of course, a negative number is added to the sum of the others) to obtain the value of the discriminant function for any individual. Individuals for which the function is greater than 0.74 are form A, or less than 0.72 are form C; about 5 per cent. of specimens are intermediate (*i.e.* with values between these limits). Examination of fig. 25 will show the relatively small overlap in the value of the function compared with wing-length (23/132 specimens) or number of hamuli (70 per cent. of specimens).

These calculations do not indicate what status should be accorded to the two forms. To do this would require nest material of both sexes from various localities. For the present, it is probably sufficient to refer to them as forms "A" and "C."

FORM A.

Female (72 examined). Testaceous; mesonotum blackish (54), brown (15) or testaceous (3), with distinct (16), faint (20), or no (36) yellow discal lines; antennae with segments 1-9 above and 2nd axilla of fore-wing blackish-brown; the following markings are pale yellow (or, in some Colombian and Guiana specimens, nearly white): a transverse mark behind the ocelli (except in 5 spec.), most of outer orbits, pronotal keel and shoulders back to the posterior margin or (in 22 spec.) only part of the way back, dorsal half of prepectus, spot below mesepimeron (except in 18 spec.), scutellum (edges brown in 1 Peruvian spec.), postscutellum, small elongate spot at bottom of metapleuron and metapleural propodeal suture (more in this region in some Peruvian spec.), large divided or (3 spec.) undivided spot on propodeum, postpetiole and abdominal tergites 2-6, except extreme sides (tergites 1-6 and sternites 2-4 with pale posterior bands in 2 Parà and 4 Peruvian spec.); abdomen considerably "frosted" with white pubescence; wings light reddish-brown, tegula with inner margin yellow or (36 spec.) mainly yellow.

Value of discriminant function 0.721-0.856, mean 0.7961; length of fore-wing 15.75-18.75, mean 17.27 ± 0.69 mm.; hamuli 15-20, mean 17.38 ± 1.34 ; length of 1st abdominal tergite 3.39-4.28, mean 3.886 ± 0.218 mm.; ratio of width/length of 1st abdominal tergite 0.364-0.458, mean 0.407 ± 0.0205 ; eye/tempora ratio 0.803 ± 0.084 ; all these characters (except eye/tempora ratio) differ significantly from form C ($P < 0.01$).

Male (8 examined, picked out on form of aedeagus only). Testaceous; mesonotum black or browner (3 spec.); antennal segments 1-10 above, and 2nd axilla of fore-wing darker; yellow are: clypeus, ocular sinus, transverse line on occiput, outer orbits, pronotum behind its keel (not reaching tegula in 1 spec.), traces of four mesonotal lines (strong in 1 spec., absent in 2), inner streak on tegula (more in 1 spec.), dorsal half of prepectus, moderate spot below the mesepimeron (except 1 spec.), scutellum and postscutellum ill-defined dorsal and ventral spots on metapleuron, large oval areas, fused above, on propodeum, posterior third of abdominal tergite 1 (posterior quarter in 1 spec.), tergite 2, except sides posteriorly (only proximal quarter in 1 spec.), ill-defined marginal bands on tergites 3-6 and most of tergite 7 (or, in 1 spec., these parts entirely testaceous); abdomen very little "frosted" with white pubescence except in the 2 Colombian spec.

Length of fore-wing 14.25-17.25, mean 16.06 ± 1.03 mm.; hamuli 14-17, mean 16.1 ± 1.36 ; length of 1st abdominal tergite 2.95-3.90, mean 3.61 ± 0.31 mm.; 1st tergite ratio 0.410-0.477, mean 0.448 ± 0.0226 .

Specimens examined:—BRITISH HONDURAS: Punta Gorda, ii.1932, ♀, vi.1932, 13 ♀, vii.1932, 4 ♀, viii.1932, ♀, x.1932, ♀, iii.1933, ♀, xi.1933, ♀ (*J. J. White*); Rio Temas, viii.1935, ♀ (*J. J. White*); Columbia, iii.1933, ♀ (*J. J. White*). PANAMA: Coiba, 31.viii.1924, ♂ (*L. E. Cheesman*); Canal Zone, 21.viii.1920, ♂ (*P. E. Cheesman*); Porto Armullis, vii.1934, ♀ (*F. Peak*); La Chorrera, 2 ♀; Panama, 1924, 2 ♀ (*L. E. Cheesman*). COLOMBIA: Magdalena Valley, El Banco, ♂, 3 ♀ (*C. Allen*); Magdalena Valley, Baranquilla to El Banco, vi.–vii.1934, ♂, 2 ♀ (*C. Allen*); Magdalena, R. Frio, 15.xii.1926, ♀ (*G. Salt*); no precise locality, 2 ♀ (Weston coll.). PERU: Valle Chanchomayo, 800 m., 1939, 10 ♀ (*W. Weyrauch*); R. Urubamba, Santa Ana, 1100 m., 1940, 6 ♀ (*W. Weyrauch*). BRITISH GUIANA: New River, 750 ft., 15–25.ii.1938, ♂, ♀, 16–17.iii.1938, ♀ (*C. A. Hudson*); Upper Courentyne, ix.1935, ♀ (*G. A. Hudson*); Oronoque—New River heads, 1935, ♀ (*H. Beddington*); Potaro R., Kaieteur Savannah, 2.ix.1937, 2 ♀ (*Richards and Smart*); Cuyuni R., Kamaria landing, clearing, 20–24.xi.1929, 3 ♀ (*Oxford Univ. Exped.*); North-west district, Issororo, xii.1918, ♀ (*G. E. Bodkin*). BRAZIL: Lower Amazons, Guaruja, 25.i.1896, ♂ (*E. E. Austen*); Pará, 4 ♀ (*A. M. Moss*), ♂, ♀; no precise locality, ♂, 3 ♀ (*F. Smith coll.*). PARAGUAY: Alto Parana, Pto. Bertoni, viii.1900, ♀ (*Bertoni*).

Form C.

Female (60 examined). Testaceous; mesonotum blackish (40 spec.), brown (7 spec.) or testaceous (13 spec.), usually without discal lines, but with them in 3 spec., and with short side-lines as well in 6 more; antennae blackish-brown with about the last 3 segments pale; the following markings are pale yellow tending to be white in some British Guiana specimens: a transverse mark sometimes occupying the whole area behind the ocelli; most of outer orbits except 1 spec. in which there is only a small ventral spot; pronotal keel and usually areas behind it back to the tegulae (except 8 spec.); dorsal half of prepectus and usually a more or less large area below the mesepimeron (except in 13 spec.); scutellum and postscutellum, except in 1 spec.; a small elongate spot at bottom of mesopleuron except in 10 spec.; metapleural-propodeal suture except in 6 spec.; large undivided (6 spec.) or divided (53 spec.) or small spot (1 spec.) on propodeum; postpetiole and abdominal tergites 2–6 (except extreme sides) or in 3 spec. with posterior margins of tergites paler banded; abdomen usually considerably “frosted” with white pubescence except in 10 spec. Wings light reddish-brown, 2nd axilla of fore-wing blackish, tegula with inner margin yellow (43 spec.) or mainly yellow (17 spec.).

Value of discriminant function 0.619–0.740, mean 0.6875; length of fore-wing 13.75–16.25, mean 15.08 ± 0.55 mm.; hamuli 12–18, mean 14.80 ± 1.27 ; length of 1st abdominal tergite 2.92–3.84, mean 3.43 ± 0.76 mm.; ratio of width/length of 1st abdominal tergite 0.369–0.580, mean 0.463 ± 0.0431 ; eye/tempora ratio 0.830 ± 0.089 ; all these characters (except eye/tempora ratio) differ significantly from form A ($P < 0.01$).

Male (8 examined, picked out on form of aedeagus only). Testaceous; mesonotum darker to dark brown in 4 spec.; antennal segments 1–9 above, and 2nd axilla of fore-wing dark; ocellar patch darker in 4 spec.; yellow are: clypeus, ocular sinus, inner and outer orbits, transverse mark on occiput, pronotum behind its transverse keel (or almost all of it in 3 spec.), 4 lines on mesonotum, inner margin (7 spec.) or most (1 spec.) of tegula, dorsal half of prepectus, very large area below mesepimeron (except 1 spec. in which area is small), scutellum (except 1 spec. in which it has only yellow spots), postscutellum (except posterior half in 1 spec.), almost whole metapleuron, propodeum except areas near spiracles, whole dorsal surface of abdomen (except 2 spec. in which tergites 2–5 have considerable testaceous marks, and 1 spec. in which only sides of tergites 1 and 7 have

yellow spots); abdomen considerably "frosted" with white pubescence except in the specimen in which it is mainly testaceous.

Length of fore-wing 14.25–16.75, mean 15.19 ± 0.80 mm.; hamuli 13–19, mean 14.9 ± 1.46 ; length of 1st abdominal tergite 3.05–3.64, mean 3.40 ± 0.204 mm.; ratio of width/length of 1st abdominal tergite 0.457–0.513, mean 0.475 ± 0.0204 .

Specimens examined:—COLOMBIA: Cali, ♂; R. Magdalena, Baranquilla to El Banco, vi.–vii.1934, ♂ (*C. Allen*). B.W.I., TRINIDAD: Mt. Harris, ♀ (*C. L. Withycombe*); St. Augustine, 2.ix.1924, ♂ (*C. L. Withycombe*); no precise locality, 5 ♀. VENEZUELA: ♀ (*G. A. Smith*). BRITISH GUIANA: New River, 750 ft., 15–25.ii.1938, 2 ♀, 750–900 ft., 28–3.iii.1938, ♀ (*C. A. Hudson*); Confluence of Oronoque and New R., 650 ft., ix–xii.1937, ♂, 4 ♀ (*C. A. Hudson*); Amazon-Courentyne divide, R. Oronoque head, 1937, ♀; Upper Courentyne, ix.1935, 2 ♀ (*G. A. Hudson*); Upper Courentyne, King Frederick William IV Falls, xi.1935, ♀; Kutari Sources, 10 i.–10.ii.1938, 2 ♀ (*C. A. Hudson*); Potaro R., Kaieteur Savannah, 5–8.ix.1937, 2 ♀ (*Richards and Smart*); North-west district, Issororo, xii.1918, ♀ (*G. E. Bodkin*). BRAZIL: R. Negro, Manacepruru, vii.1935, 31 ♀ (*G. V. Vredenburg*); Teffé, 26.ix.1904, ♂ (*A. Ducke*); Prov. Pará, Santarem, vi.1935, ♀ (*G. V. Vredenburg*); Pará, ♀ (*A. M. Moss*); Lower Amazons, Guarupa, 1896, ♂, Brèves, 16.i.1896, ♂ (*E. E. Austen*); no precise locality, 2 ♀ (*F. Smith coll.*), ♂, ♀. PERU: Valle Chanchomayo, 800 m., 1939, 2 ♀ (*W. Weyrauch*).

5. *Apoica arborea* de Saussure.

Female (22 examined). Testaceous; mesonotum, disc of vertex from top of clypeus to occiput, 2nd axilla of fore-wing, anterior 6th and axillae of scutellum, black; bright, rarely whitish; yellow are: ocular sinus, oblique spots behind ocelli, band (not touching eyes) along middle of tempora, separated spots on each side of pronotum and (1 spec.) a dot on the fovea, dot at extreme base of costa and 1st axilla of fore-wing, top half of prepectus, scutellum and postscutellum, narrow bands at posterior margins of tergites 1–6, and sternites 2–3 (18 spec.), 2–4 (1 spec.), 2–5 (3 spec.). Tegula dark brown, with inner yellow dot in 2 spec., or inner yellow streak in 5 spec.; wings orange-brown tinged. Antennae brown, segments 3–6 or 3–7 blackish, 8–12 whitish yellow. Length of fore-wing 11.75–13.75, mean 12.77 ± 0.50 mm.; hamuli 11–14, mean 12.73 ± 0.84 ; length of 1st abdominal tergite 2.55–3.05, mean 2.80 ± 0.134 mm.; ratio width/length 1st abdominal tergite 0.535–0.641, mean 0.560 ± 0.0363 ; eye/tempora ratio (10 measured), 0.740–1.128, mean 0.893 ± 0.117 .

Male (1 spec. examined). Testaceous; suffusion above antennal segments 1–7, disc of vertex between and in front of ocelli, mesonotum, 2nd axilla of fore-wing, patch in centre of 1st abdominal tergite, black. Clypeus, inner and outer orbits, occiput, most of pronotum (except large patch on sides posteriorly), 2 long central and 2 short lateral mesonotal streaks, inner margin of tegula, upper half of prepectus, most of mesepisternum below epimeral plate, scutellum and postscutellum, rather small patches on each side of propodeum, narrow posterior bands on abdominal tergites 1–6 and sternites 2–6, most of segment 7, yellow; abdomen not "frosted" with white pubescence.

First abdominal tergite not so much broadened as in female, length 3.03 mm., width/length ratio 0.498. Antennal segment 13 twice as long as broad, flagellar segments distinctly knotted. Clypeus with ventral margin angular. Scutellum and postscutellum with only very short inconspicuous pubescence. Genitalia (figs. 17–19) with the distal end of the paramere pointed, cuspis almost straight, distal part of aedeagus straight, narrow and parallel-sided, ventral lateral median processes conspicuous, rounded, blackened. Length of fore-wing 14.25 mm., hamuli 13.

Specimens examined :—BRITISH GULANA : North-west district, Issororo, vi.1915, ♀ (*G. E. Bodkin*); Potaro R., Kaieteur Savannah, 8.ix.1937, ♀ (*Richards and Smart*); Mazaruni R., Hills Estate, 10.iv.1926, 2 ♀ (*L. A. Cleare, Jr.*); New R., 750 ft., 26-27.iii.1938, 8 ♀, 20-23.iii.1938, 3 ♀ (*C. A. Hudson*); Confluence of Oronoque and New R., 650 ft., ix.-xii.1937, ♂, ♀; Amazon-Courentyne divide, head Oronoque R., 1937, ♀; Kutari Sources, 10.i.-10.ii.1936, ♀ (*G. A. Hudson*). BRAZIL : Pará, 3 ♀ (*A. M. Moss*); Amazons, ♀ (*F. Smith coll.*).

20. APPENDIX 3.

Observations on Colonies of *Polistes* and *Belonogaster*,

Sent from Natal by Dr. R. F. Ewer.

By O. W. RICHARDS.

Through the kindness of Dr. R. F. Ewer I recently received some wasps' nests from Natal. They had been collected in the evening when probably most of their inhabitants were at home; the nests and wasps were preserved in formalin. An attempt was made to dissect all the wasps to examine the development of the ovaries, but in some nests the abdominal contents were not well preserved. Two collections were made: one in Drakensburg Mts., Champagne Castle, 7000 ft., 4.ii.1947 (= A), the other at Maritzburg, 2128 ft., 15.iv.1947 (= B). From information supplied by Dr. Ewer, it appears that both localities have a relatively cool, dry period in June-August. At Cathkin, 4152 ft., in the next valley to Champagne Castle, the mean monthly temperatures vary from 51.7° F. (July) to 68.3° F. (January), with a mean of 67.5° F. in February. The mean monthly rainfalls are 0.11 in. (June), 9.35 in. (February) and 10.02 in. (January). At Maritzburg the mean monthly temperatures are 56.1° F. (July), 73.5° F. (February) and 67.5° F. (April), and the rainfalls 0.55 in. (August), 5.87 in. (February) and 2.25 in. (April).

Three species were represented in the collection:

1. *Belonogaster griseus* (Fab.) (approaching var. *fuscipennis* R. du Buyss.).

Nests 1-2 (A), nests 3-6 (B).

Nest 1. About 200 cells; a large and compact central comb, mostly of capped cells, surrounded at a lower level by a more or less complete ring of very shallow cells, many of which were empty. There were present 2 ♂, 29 ♀, about 20 eggs (in the shallow cells), 128 larvae (28 large) and about 50 spun larvae or pupae. The abdominal contents of the females had disintegrated.

Nest 2. A small nest without parent wasps, but with one cocoon and one dead larva. It contained an extraordinary Myrmedoniine beetle, *Zyras* sp., possibly new, (STAPHYLINIDAE) (det. Dr. Hugh Scott, F.R.S.).

Nest 3. A nest of about 70 cells, 3 capped, but apparently no brood or eggs. These had probably been destroyed by Muscid larvae which had bored right through the bases of many cells. Many empty and 3 full puparia were present. There were 1 ♂, 12 ♀ wasps, of which 4 were workers (or possibly intermediates) and 8 were queens (3 or more ripe eggs present).

Nest 4. There were 3 large cells (2 capped) and about 50 very shallow ones,

but, apart from one large larva and one pupa, very little brood. Two empty Muscid puparia were found in the cells. Five female wasps were captured; 2 with ovarioles filamentous (= workers), 1 with small egg-rudiments (= intermediate), and 2 with at least 3 large eggs (= queens).

Nest 5. This had 21 small, very shallow cells, 6 with eggs. There were 3 ♀ wasps which had at least 6 ripe ovarial eggs (*i.e.* one per ovariole).

Nest 6. This had 65 cells, those near the petiole being short and those furthest from it long and, in two cases, capped; the majority contained small larvae. The adult wasps consisted of 4 ♂, 16 ♀, 7 ♀. The workers were smaller and had fewer hamuli than the queens, but the differences were not significant, even when the data of nests 3-6 were taken together.

2. *Polistes marginalis* Fab. (det. Dr. J. Bequaert).

Nests 7-9 (A).

Nest 7. This consisted of a very irregular comb of about 105 cells of all sorts of lengths, the brood-stages being scattered at random. The petiole seemed to be very eccentric. There were about 10 eggs, 20-30 larvae (mostly small), and 19 cocoons; many cells were empty. The wasps present were 8 ♂, 2 queens (ovaries quite well developed but details obscure) and 5 workers (ovarioles filamentous).

Nest 8. The comb of 126 cells, the peripheral ones mostly short, was fastened to a twig by two petioles, one central, the other very near the edge of the comb. There were about 23 eggs (some in large cells being used a second time), 40 larvae and 24 cocoons. There were 15 ♀ wasps, 2 queens (ovaries more or less well developed, one with $20 \pm$ eggs), 1 intermediate (ovarioles a little developed), 12 workers (ovarioles filamentous).

Nest 9. This was a very fragmentary nest, with little brood. There were 2 wasps, a worker and an intermediate.

If nests 7 and 8 are taken together, there are 4 ♀ and 17 ♂ available for comparison. The mean wing-lengths and hamuli numbers were: ♀ 9.9 mm., 12.0; ♂ 9.3 mm., 10.8. Larger numbers would be required to decide whether the differences are significant.

3. *Polistes smithii* de Saussure.

Nest 10 (B). The subcircular comb, with central petiole, had 124 cells, 28 capped and these nearly all peripheral. Most of the cells contained rather small larvae, but some were large and some of the capped cells contained pupae. There were 2 ♂, 51 ♀ wasps; the females apparently all had filamentous ovarioles, but a few were in too bad condition to be sure.

As far as is known, all VESPIDAE, except the VESPINAE, have three ovarioles a side, and this is true of the species dealt with above. A single worker of *P. smithii*, however, distinctly had four a side, but this seems to be only a freak, as three a side could be made out in nearly all the others.

DISCUSSION.

These observations, as far as they go, support those of Roubaud (1916). *Belonogaster* clearly differs from most S. American Polybiines in the small proportion of females with filamentous ovaries, while the queens are of a type

equivalent to the "intermediates" in other genera. In *Polistes marginalis*, also, two nests both apparently had two egg-laying females. Better preserved material would be required for a more detailed study of ovarian development.

21. SUMMARY.

1. An introductory account is given of the S. American social wasps and of the architecture of their nests. Later, those recorded from British Guiana are treated in more detail.

2. Most colonies differ from those of temperate climates in containing many egg-laying females and in being founded by swarms. Colonies can be classified into *haplometrotic* (with one queen) or *pleometrotic* (with more than one). The method of foundation may be by a single queen (= *non-swarming*), by several queens (possibly always sisters) arriving at the nest-site together or at intervals (= *association*), or by one or more queens accompanied by workers (= *swarming*).

3. The three principal types of nest-architecture are *phragmocytтарous* (new combs built on the lowest part of the envelope and pierced by the exit-hole), *stelocytтарous* (combs suspended one below the other by little pillars), and *astelocytтарous* (new term: combs fixed direct onto trunks of trees, etc.). It is suggested that nest-architecture must be used with great caution as a guide to affinities.

3. Colonies founded by swarms quickly reach a certain size, the *initial colony*, before the first brood emerge; with the advent of new workers another period of growth may ensue. Colonies may persist for a rather short period (about three developmental cycles) or for much longer. The reason for the break-up of many colonies so soon in tropical conditions is obscure, but it may be remembered that even in *Vespula*, in temperate climates, the end of the colony often precedes the onset of autumn. In the short-lived type of colony an estimate can be made of the age of the nest in terms of the developmental period.

4. While the castes are poorly developed compared with those of such social insects as the ants, it is shown that even in the VESPIDAE the subject is more complicated than has been supposed, chiefly owing to various secondary modifications of the queen and worker type. Many colonies of POLYBINAЕ contain *intermediates*, i.e. unfertilised females with partially developed ovarioles. Differences in skeletal structures of queens and workers can often be demonstrated biometrically; intermediates are usually intermediate in skeletal structures. This suggests that caste-differentiation must be due to some difference of treatment in the pre-adult stages.

5. Factors which may contribute to caste-differentiation are reviewed. It is difficult as yet to reach any very firm conclusions, but special emphasis is placed on the larva/worker ratio. In the least differentiated types, changes in this ratio with the growth of the colony may suffice to explain queen production.

6. The South American Polybiine colonies studied were found to be of three types (not closely connected with the position of the genus in the taxonomic system). Type I—queens rather few, often only one. Intermediates rare and most frequently found in nests with one or few queens. Type II—queens usually numerous. Intermediates abundant and grading into queens in all

characters except fertilisation. Type III—*Mischocyttarus* with very small colonies often of one queen and less than half a dozen workers.

7. The relations of wasps to ants are reviewed and it is suggested that in the tropics, where ants are always very numerous, they may have played a substantial part in the evolution of wasp-colonies.

8. The records of Strepsipterous parasites of the POLYBIINAE are collected. A new type of male parasite is briefly described.

9. In the short-cycle POLYBIINAE it is shown that the rate of cell construction is related to the rate of oviposition (and not vice versa). If the developmental period is 21 days, the number of cells constructed per worker per day $= r = 0.3986 + 0.0119q$ (where q is the number of queens in the nest). It is shown that the rate of oviposition depends to a considerable extent on the number of queens in the nest.

10. Rough estimates have been made of the *productivity* (new queens per old queen) and of the *efficiency of reproduction* (new queens per old queen per day) in several genera of VESPIDAE. The usual value of the second parameter seems to be about 0.07, but in some VESPINAE it may be nearly 0.50.

11. The probable mode of evolution of social life in the VESPIDAE is examined. The early stages of the process are still obscure but they probably involved the change from mass- to progressive-provisioning; this may have been induced by some change in the oviposition-cycle of the female. A considerable increase in the length of the life of the female would also have been necessary, and it is probable that most of the process must have occurred under tropical conditions.

12. Once a real social unit with queens, workers and males has been evolved it is possible to examine algebraically the conditions for maximum efficiency, particularly in the partition of females between queens and workers, and between one new nest and several.

13. The efficiency of reproduction is independent of the number of workers in the founder-swarm, provided enough queens are present to keep all the workers busy. This conclusion, however, would not hold if, for the purposes of defence, it was desirable for a certain minimum size to be passed as rapidly as possible.

14. If likely numerical values are given to the developmental period (21 or 30 days) and to the length of life of the worker (35 or 45 days), if r (cells/worker/day) is given the value calculated from the nest-data (see conclusion 9), and if the founder-swarm is taken to consist of 130 individuals (about the mean for all colonies of short-cycle POLYBIINAE), it is then possible to calculate the value of q (number of queens) which would give maximum efficiency. The observed value was 15.9, and the calculated values corresponding to the two sets of constants were 15.75 and 16.0.

15. It can be shown, with certain assumptions, that in short-cycle POLYBIINAE the most efficient way to partition a fixed number of queens and workers available for colony foundation at the end of the cycle, is to found as many colonies as is consistent with having the right proportions of queens and workers. This conclusion might, however, be modified by the needs of defence or of temperature control.

16. Considerations such as these may suffice to explain the occurrence of the various types of colony which have been observed in nature.

17. It can be shown that, provided the worker lives longer than the developmental period, the larva/worker ratio, after reaching a maximum at the end of the first developmental period tends to fall continuously in a fluctuating manner.

18. In Appendices 1 and 2 the taxonomy of the species of *Polybia* allied to *P. occidentalis* (Oliv.), and of the species of *Apoica* Lep., is reviewed.

19. Appendix 3 includes observations on colonies of two African species of *Polistes* and of one species of *Belonogaster*.

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EXPLANATION OF PLATES 1-4.

PLATE I. Figs. 1-8.

- FIG. 1. *Protopolybia holoxantha* (Ducke), nest 83.
 2. *Protopolybia minutissima* (Spin.) var. *binominata* (Schulz), nest 168. Scale — 1 + 1 inches.
 3. The same, nest 57.
 4. The same, nest 211.
 5. *Protopolybia pumila* (Sauss.), nest 302.
 6. The same, closer view after removal from tree.
 7. *Brachygastra scutellaris* (Fab.), nest 180.
 8. The same, closer view.

PLATE II. Figs. 9-18.

- FIG. 9. *Metapolybia cingulata* (Fab.), nest 311, on cowshed.
 10. The same, closer view.
 11. The same, nest 11, on *Eucalyptus* trunk.
 12. The same, opened up.
 13. Nests of *Polybia rejecta* (Fab.) on mango tree, together with those of *Dolichoderus*.
 14. The same, another view.
 15. The same, nest 4609 with envelope partly removed. (Photo: J. E. Duffield.)
 16. *Polybia occidentalis* s.sp. *platycephala* Rich., nest 310.
 17. The same, closer view.
 18. The same, nest 10 with the side removed.

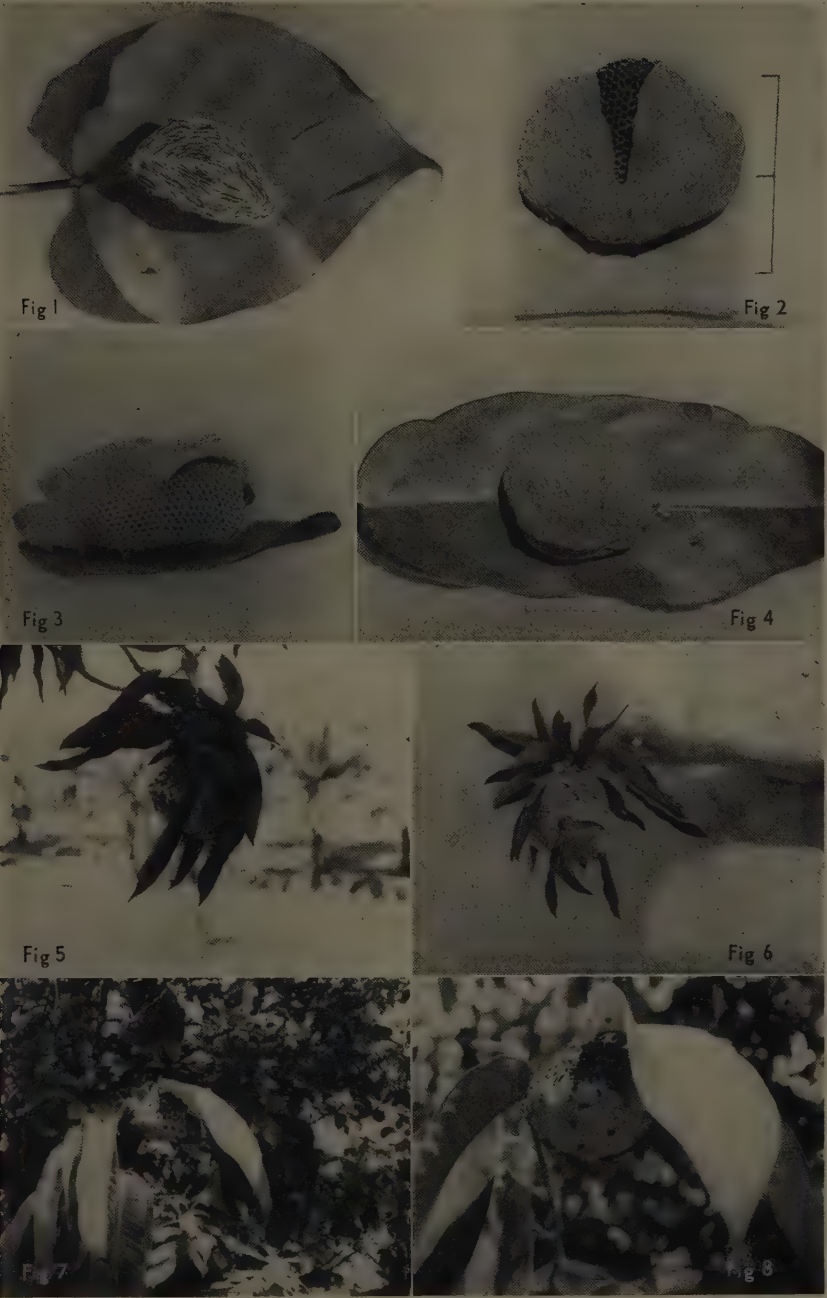
PLATE III. Figs. 19-27.

Scale, where included, = 1 + 1 inches.

- FIG. 19. *Polybia bistriata* (Fab.), nest 164, ventral view.
 20. The same, lateral view.
 21. The same, the envelope removed.
 22. *Polybia bicyttarella* Rich., nest 104.
 23. The same, nest 162.
 24. The same, nest 41.
 25. *Apoica albomaculata* (Fab.), nest 1368. (Photo: J. E. Duffield.)
 26. *Stelopolybia fulvofasciata* (Deg.), fallen tree trunk with some wasps clustered round the entrance of nest 338.
 27. *Stelopolybia pallens* (Lep.), nest 223 on liane.

PLATE IV. Figs. 28-37.

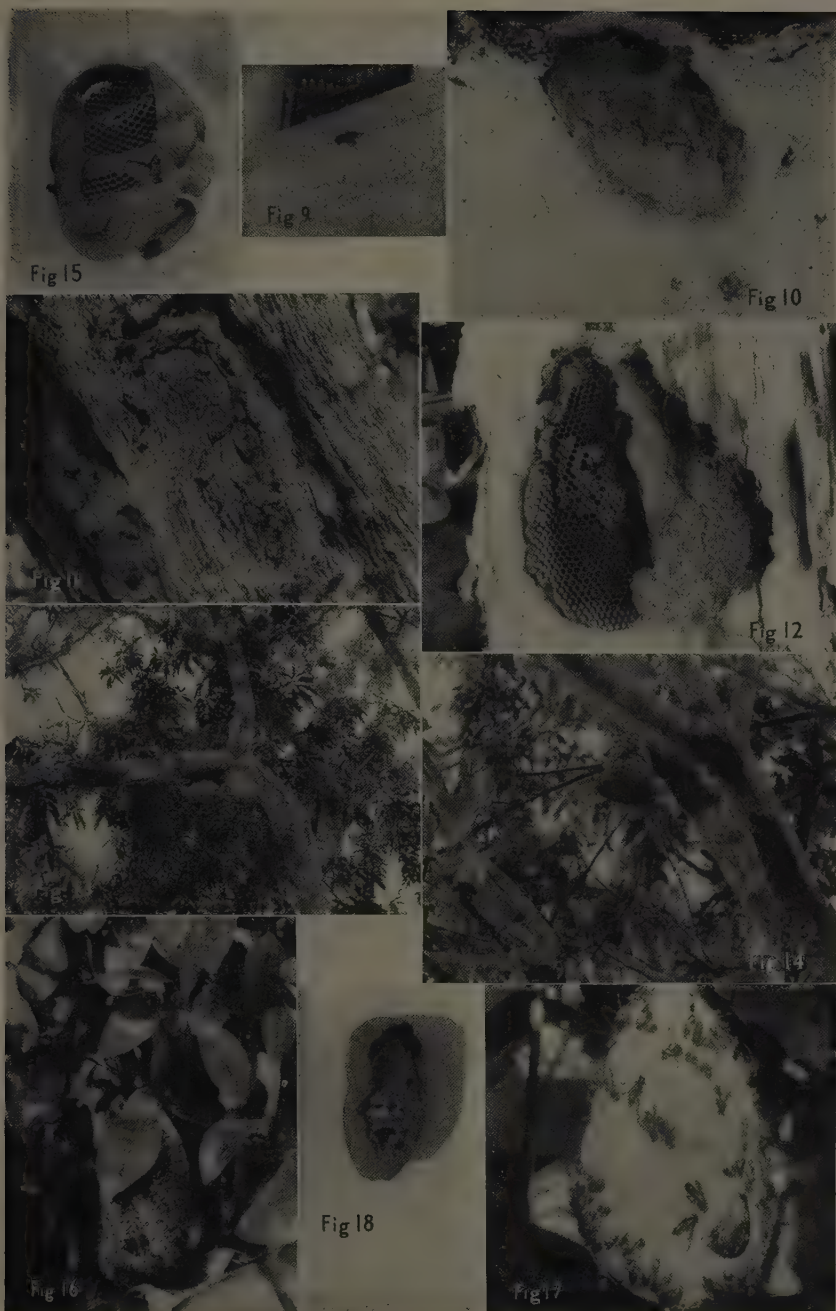
- FIG. 28. *Stelopolybia pallens* (Lep.), nest 106, which was abnormal in having two entrances.
 29. The same, nest at Moraballi Creek with envelope partly removed. (Photo J. E. Duffield.)
 30. *Parachartergus fraternus* (Grib.), colony 235, first nest.
 31. The same, another view.
 32. The same, first nest being taken to pieces by the wasps.
 33. The same, the second nest being constructed.
 34. *Polistes carnifex* (Fab.), general view of nest 161.
 35. The same, closer view of the nest on *Clusia* sp.
 36. The same, ventral view of the detached comb showing all the early stages.
 37. *Polistes canadensis* (L.) var. *cinctus* Lep., two nests on roadside bank, St. Vincent.
 A nest of *Sceliphron fistulare* (Dahlb.) (SPHECIDAE) is visible beneath them.



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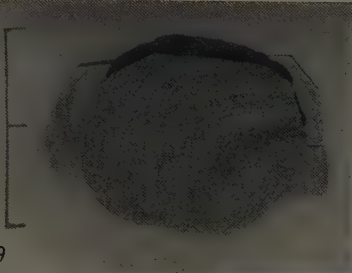


Fig 19



Fig 20



Fig 22



Fig 23



Fig 24

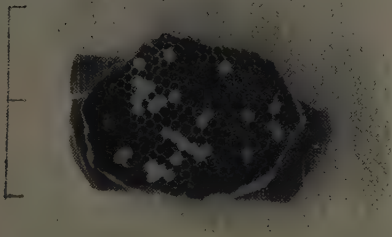


Fig 21

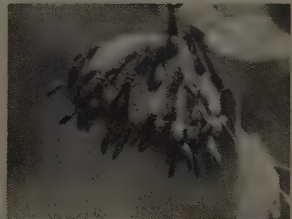


Fig 25

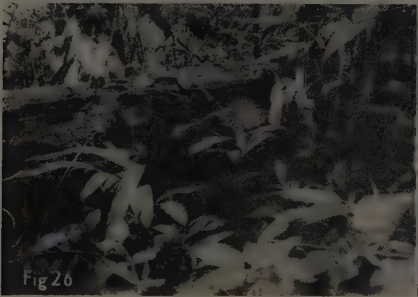


Fig 26

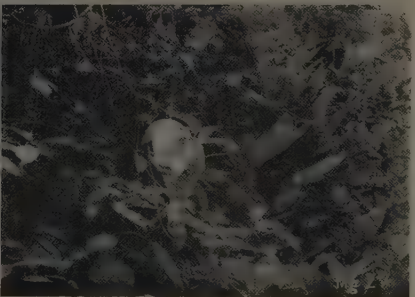


Fig 27

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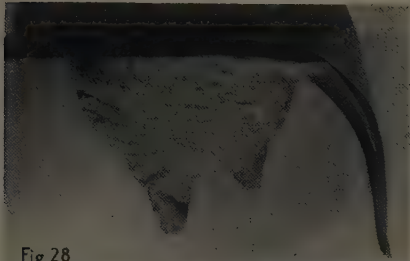


Fig 28



Fig 29

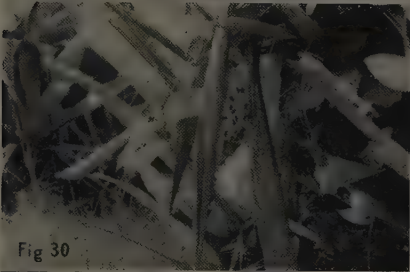


Fig 30

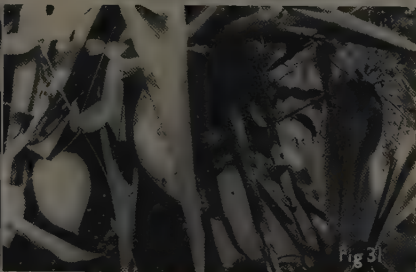


Fig 31

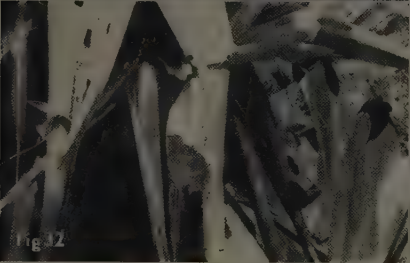


Fig 32

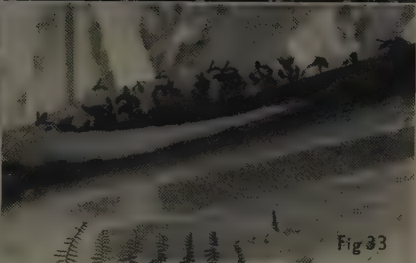


Fig 33



Fig 34



Fig 35

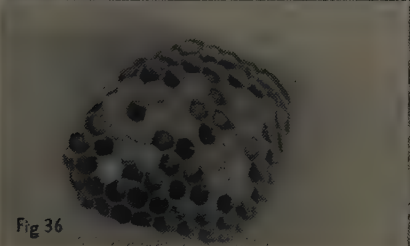


Fig 36



Fig 37

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AN INTRODUCTION TO A CLASSIFICATION OF THE AVIAN ISCHNOCERA (MALLOPHAGA): PART I.

By THERESA CLAY.

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INTRODUCTION.

AN attempt to make a key for the genera of the Ischnocera on the lines of that made for the Amblycera (Clay, 1947) has presented many difficulties. These are mainly caused by the amount of convergent and parallel evolution which has taken place in this superfamily, resulting in those characters which could be used in such a key being found in unrelated genera. It is necessary, therefore, to make a more thorough study of both the external and internal anatomy with a view to finding reliable characters on which to base a classification, and to review the distribution and variability of those characters on which the genera have previously been based. The basic characters of the internal and external morphology are, in general, remarkably uniform throughout the Ischnocera, but superficially there are considerable differences in the proportions of the body and the development of sutures and of secondary lines of thickening. These differences are reflected in the large number of genera (over 130) which have been described, many of which grade into each other, or can hardly be regarded as more than well-marked species groups. Elsewhere (Clay, 1949) it has been suggested that the Ischnocera acquired these basic characters early in their evolution, possibly while the birds had a more uniform feather covering and before their divergence into different groups with the ensuing modifications of the feather structure. The more superficial characters on which the genera of the Ischnocera are based are mainly those which are adaptive to the different ecological niches on the body of the bird, and possibly to the different feather structure characterizing the particular group of hosts. During this evolution there was much convergence and parallelism, resulting in the original relationship between the genera being in many cases obscured. Thus an attempt to arrange these genera in families on the characters usually employed gives groups containing a heterogeneous collection of genera and obviously of polyphyletic origin.

The genus.—Since there will be frequent references to characters being of generic importance and as the generic concept is mainly a subjective one, it is necessary to state the principles on which genera have been recognized or discarded in this series of papers. The generic category is used for a convenient grouping of similar species of common phylogenetic origin. It is inherent in the generally accepted theory of the evolution of the Mallophaga that similar species from related hosts are themselves related. Throughout the great majority of the Ischnocera this fact is so obvious that it needs no emphasis—the exceptions to this general principle have been summarized and discussed elsewhere (Clay, 1949). This secondary check on the relationships of species

of Mallophaga based on the relationships of their hosts is naturally of the greatest value, but where the principle is applied indiscriminately it may lead to considerable errors in classification. Thus, genera are now being erected for groups of species morphologically indistinguishable from the remaining species in the genus merely because they parasitize a distinct group of hosts.

Two types of genera based on their origins can be distinguished in the Ischnocera. These are the end-products of the processes of speciation which brought about one, the allopatric species, and the other, the sympatric species; the origin and evolution of these have been discussed elsewhere (Clay, 1949).

The allopatric genus comprises a number of species formed as a result of the isolation and divergence of their hosts (Clay, 1949 : 288); this has resulted in the parasites of an order, family or genus of hosts resembling each other more closely than the corresponding species of a different order, family or genus of hosts. It is, therefore, a matter of opinion whether the genus should include the small group of similar forms from the genus of hosts (frequently a polytypic species), or the larger group of less similar forms from the host family (superspecies or sometimes polytypic species), or the still larger and more diverse group of species from the host order. Naturally the cases of all parasitic groups and all host divisions are not analogous. Parasitic groups, which seem either to be more plastic or to parasitize ancient orders of birds where the hosts have been longer isolated and are more divergent, tend to show a greater amount of divergence between the species, or to contain aberrant species, or species with exaggerated dimorphism of the secondary sexual characters. Such groups of species encourage the erection of a large number of small genera, many of which are monotypic; and although these genera come within the definition of a group of similar species of common phylogenetic origin, they cannot be considered as convenient groupings. This erection of genera for polytypic or superspecies merely burdens the memory with names which give no clue to relationships, in many cases makes it impossible to place a species if only one sex is known, and probably means the future erection of further monotypic genera for the inclusion of new species.

The present writer agrees with Mayr and Delacour (1945 : 5): "We believe in large genera, since it is the function of a generic name to express relationship (as an aid to memory), not distinctness, which is expressed by the species." Unfortunately many workers on Mallophaga seem to be concentrating on obscuring as many natural relationships as possible, superspecies, polytypic species and even aberrant members of a superspecies being made into genera. This results in the subspecies being called a species, a polytypic species a genus, a genus a family, with the ensuing multiplication of the higher categories. There would seem to be no advantage, for instance, in dividing *Degeeriella* from the Falconiformes into two genera as has been done, nor in separating the *Philopterus* species found on the HIRUNDINIDAE (a family of the Passeres) from those parasitizing the remainder of the Passeres. *Goniodes* from the Galli contains a number of species groups, and these have been used as a basis for erecting unnecessary genera (Kéler, 1940). On the other hand, *Anatoecus*, from the Anseriformes, possibly a less plastic group of parasites, shows little divergence throughout the genus. It is only by realizing that both these groups comprise forms which (with the exception of the sympatric species) are geographical (or host) replacements of each other, and in the case of some groups could be included in one polytypic species or a

superspecies, that one can get a satisfactory generic concept in the Mallophaga.

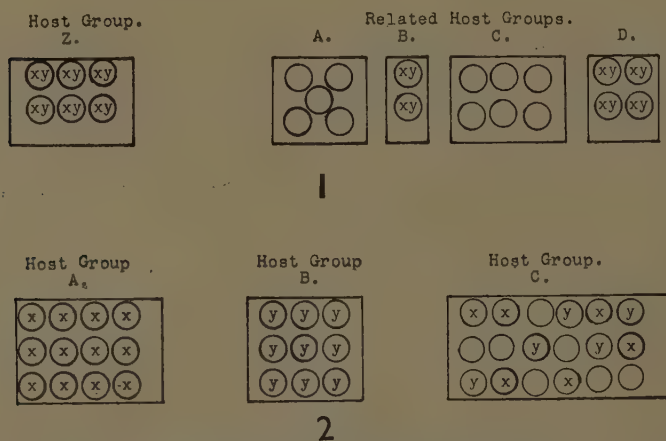
Host distribution is of importance as a secondary check on the relationship between species and on the delimitation of genera. If, for instance, a genus is erected for species from a certain host group, but is based on characters which means the inclusion also of some of the species parasitizing not closely related hosts, then such a group does not contain a natural association of related species and does not come within the above definition of a genus. Such a case is illustrated graphically in fig. 1: z is one host group; A , B , C and D are four host groups related to each other. The species on all groups are similar, but those on z , B and D can be separated from those on A and C by certain characters (x and y). It is not permissible to use these characters to erect a genus to include the species found on z , B and D because the species on the $A-C$ group of hosts must be more closely related to each other than any of them are to those on z (it is assumed that secondary infestations from z to B and D have not taken place). All the species on the five host groups must be included in one genus. The separation of *Clayiella* from *Philopterus* and some of the genera based on colour pattern (*Koeniginirmus* and *Docophorulus*) are such cases. The host distribution of the only two species included in *Kodocephalon* by K  ler (1940), namely *Goniodes suborbiculatus* from a species of COLUMBIDAE and *Goniocotes discogaster* from a species of the MEGAPODIDAE (Galliformes), suggests that this is not a natural association and is not, in fact, supported on morphological grounds.

On the other hand, a consideration of the host distribution of species alone, ignoring morphological characters, also results in the erection of untenable genera. An example of such a case is illustrated in fig. 2: three unrelated host groups A , B and C are parasitized by similar species of Mallophaga. The species on A show a certain character x , and those on B a character y , and of those on C (a much larger group of hosts with a greater number and diversity of species) some show character x , some y , and some neither of these characters. It is not permissible to use characters x and y as a basis for separating generically those species found on host groups A and B even though all three host groups are unrelated to each other. The separation of *Furnaricola* from *Rallicola* is such a case.

ALLOPATRIC GENERA.

In the majority of allopatric genera the host order or suborder forms a clear-cut line between groups of species and gives the limits of the genera—for example *Anaticola* on the Anseriformes, *Ardeicola* on the Ciconiiformes, *Falcolipeurus* on the Falconiformes. Where a genus is found on more than one host order (*Saemundssonina*, for instance, on the Charadriiformes, the Procellariiformes and the Gruidae) the species found on each host order cannot be segregated into genera unless there is a morphological basis for this. However, there are some cases of such groups of related species with a wide host distribution which raise the most difficult problem in the classification of the Ischnocera. It seems possible that in these—the *Degeeriella* complex may be used as an example—the immediate ancestor of the species groups on each host order gave rise not only to the *Degeeriella* type of species, but to others which occupied different ecological niches, and have now evolved into groups of species very different from the *Degeeriella* type to which they are most nearly related. Therefore, to include the whole *Degeeriella* complex,

comprising *Lagopoecus*, *Cuculicola*, *Picicola*, *Upupicola*, *Capraiella*, *Trogoninirmus*, *Acutifrons*, and another group from the BUCEROTIDAE, in one genus would be correct on morphological grounds, but there is a possibility that *Picicola* for instance is more closely related to another genus (*Penenirmus*) on the Passeres than to *Degeeriella*. In all cases where the distribution of a genus covers more than one host group there is the possibility that the species on one of the host groups are more closely related to another genus on that host group, although generically inseparable on morphological grounds from the species on the other host groups. This has been discussed elsewhere (Clay, 1949 : 295), and has been raised by Wood (1950 : 96) with reference to the geographical distribution of a group of rodents. It must be admitted that the present system of classification cannot satisfactorily represent such relation-



FIGS. 1, 2.—Distribution of species of Mallophaga on unrelated host groups. Explanation in text. Circles denote species of Mallophaga.

ships. However, unless there is good evidence to the contrary, genera must be based on morphological criteria and not on hypothetical speculations of their evolution based on distribution. Each of such cases must, of course, be judged individually—the wide distribution of *Saemundssoni* is most probably due to secondary infestations, whereas that of the *Degeeriella*-complex may be due to the discontinuous distribution of a once universally distributed genus.

SYMPATRIC GENERA.

The genus which is the end-product of the sympatric species presents a more difficult problem. Sympatric species are found in every stage of divergence, from those which differ only in the details of the male genitalia (the females being very similar or indistinguishable) to those which can be separated generically on well-marked characters. The degree of divergence will depend mainly on the age of the two sympatric species and whether they have taken up different habitats on the host—in the latter case such forms may now be placed in different families. Where the two species have been

subjected to the same environmental factors degree of divergence is presumably dependent on the length of time they have been separated. The question of good generic divisions in these cases is an extremely difficult one. All these sympatric species groups will come within part of the generic definition given above, that is, a group of related species, so that the question to be decided is that of convenience. Other factors being equal it is convenient to have two distinct species on one host contained in different genera, but it is not convenient to have a position where species cannot be placed if only one sex is known, nor is it convenient if the two genera grade into each other to such an extent that there are no criteria for placing some of the species in one genus rather than another. The original species of *Soricella* were so distinct from *Columbicola* that a generic division seemed justified, but a large series of species from the COLUMBIDAE shows that these two groups grade into each other to such an extent that a generic division is now impossible. If the *Goniodes-Goniocotes* complex of species are examined from a large number of host species, even the apparently well-defined genera *Goniodes* and *Goniocotes* seem to grade into each other. On the TINAMIDAE, where there is a wealth of sympatric species and genera, generic separation becomes an almost insoluble problem.

The complexity and difficulty of generic separation in these sympatric forms has led to the erection of a multiplicity of genera, either owing to the small amount of material examined, or to the fact that the alternative to a great number of small genera seems to be the inclusion of a large number of species (for example all *Goniodes* and *Goniocotes*) in one genus.

While a correct evaluation of such genera is probably not possible without a more complete series of species than is usually available, it would seem to be more satisfactory to keep the generic divisions fairly wide to include as many related forms within the same genus as possible.

MATERIAL AND METHODS.

Whole specimens have been examined after treatment by caustic potash and mounting in Canada balsam, by mounting in polyvinyl lactophenol and by staining with lignin pink or mercurochrome. Both the internal and external anatomy has been studied by dissections, and sections of examples of a small number of genera have been examined.

Although it has been possible to examine specimens of practically all the known genera, the amount of suitable material available has limited the dissection of examples of all these genera, and time has limited the number of different species of each genus dissected. However, any such attempt at the classification of the Ischnocera must be considered as tentative due to the great amount of work still necessary, not only on the morphology but also on the biology of this group, together with the limitations involved by the number of genera and species still unknown.

ACKNOWLEDGMENTS.

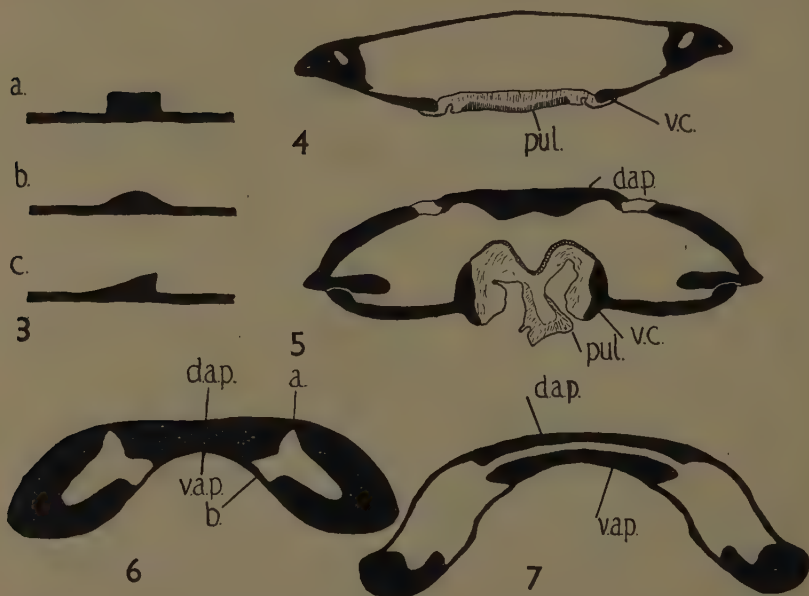
I am greatly indebted to Dr. S. Symmons and Dr. J. E. Webb for the loan of sections and to the following for providing material: Messrs. M. A. Carriker and G. H. E. Hopkins and Dr. L. R. Guimarães and Dr. H. Sick of the Fundação Brasil Central. Also to Mr. G. H. E. Hopkins for much helpful advice and criticism.

A. THE HEAD.

Terminology.

Scornful references (Cope, 1941: 72) have been made to the terminology
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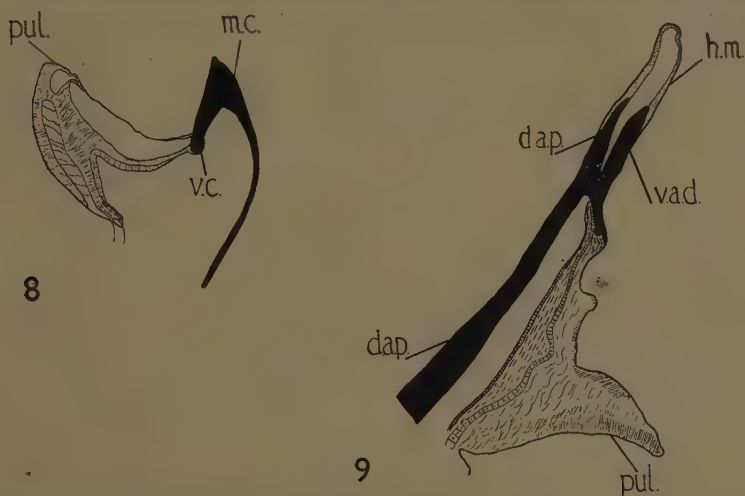
used to designate parts of the head in the Mallophaga, and a suggestion made that these should be replaced by terms with a morphological significance. This criticism would be more impressive if those working on the morphology of the Mallophagan head could agree on the homologies of the various sutures and lines of thickening which are used in the classification of the group. Until this has been achieved it seems more satisfactory to retain the names which can be understood by all workers than to follow the various ideas and theories of the homologies of different parts of the head put forward by recent morphologists. Even in the terms now in use there is little conformity, however, and it has been necessary to adopt some new names and to define and restrict those already in use. Two terms as used here must first be defined :



FIGS. 3-7.—Transverse sections of preantennal region of head. (3) Endocarinae (diagrammatic). (4) *Coloceras* sp., at level of pulvinus. (5) *Philopterus* sp., at level of pulvinus. (6) *Brüelia* sp., at level of anterior plate. (7) *Philopterus* sp., at level of anterior plate. Explanation of lettering as in figs. 10, 11.

Endocarina.—One of the most characteristic features of the Ischnocera is the presence of various dark bands running across the head. These so-called bands are internal ridge-like thickenings of the cuticula. The conspicuousness of the band is due to the thickness of the cuticula, and, as the "edges" of the band as seen in the surface view of the mounted insect are the lateral sides of the internal thickening, the definition of the band is dependent on the angle the thickening makes with the normal inner surface of the body wall. Thus a ridge which in transverse section shows these angles as right angles (fig. 3A) will appear as a very distinct band, but one in which the sides slope gently into the inner surface of the rest of the body wall (fig. 3B) will appear externally as an indistinct band. In some cases one side of the ridge may be at right

angles, and the other merge imperceptibly into the general surface (fig. 3c) so that the band is only delineated on one side. Sometimes this thickening may become less in certain areas so that portions of the bands become indistinct or apparently absent. All these types of internal thickenings are here called endocarinae or carinae. In many instances the form of some of the endocarinae are useful generic characters, but their apparent absence in other cases may have no significance—the presence or absence of the whole or part of the temporal carinae is a case in point. In some heads there may be dorsal and ventral endocarinae as well as those projecting from the lateral walls. It is not surprising, therefore, that considerable difficulty is experienced in tracing these carinae in mounted specimens, and that so many figures of Ischnoceran



FIGS. 8, 9.—Longitudinal sections of preantennal region of head. (8) *Lipeurus* sp. (9) *Philopterus* sp. Explanation of lettering as in figs. 10, 11.

heads give a composite picture partly dorsal and partly ventral. The section of a head of a species of *Philopterus* a little way anterior to the origin of the mandibles (fig. 5) illustrates the complexity of the endocarina in the more specialized forms.

Sutures.—The term suture is used here in the sense of the second definition given by Snodgrass (1935 : 53), that is, "Lines where the sclerotization of the cuticula has become secondarily discontinuous in order to give flexibility." These thinner areas are again a characteristic feature of the Ischnoceran head, and are frequently constant throughout groups of related species and may form reliable generic characters. The term is used for all such areas which appear unsclerotized in the whole insect, although in some cases (only discernible in sections) the sclerotization is thin, not actually interrupted; in mounted specimens the points (a) and (b) on fig. 6, for instance, will appear as sutures.

The General Structure of the Primitive Head and its Modifications.

It is generally assumed that the primitive Ischnoceran head had the marginal carina complete—the so-called circumfasciate type of head now

found in such genera as *Goniodes* (fig. 10), and that the sutures and form of endocarinae found in such genera as *Saemundssonina* (fig. 11) are secondary. This view is supported by the fact that in some genera in which the adults show the anterior sutures, the nymphal stages have the circumfasciate head. The more primitive type of head capsule¹ has the following general characters : The preantennal region is enclosed by a thickened rim which turns inwards immediately anterior to the antennae to form a thickening dorsally, and to fuse with the framework supporting the mandibles ventrally. Passing anteriorly from this framework each side is an endocarina which forms a semicircle in front of the prestomum and to which is attached the pulvinus, (*sensu* Cope). The pulvinus, which is a membranous lobe of characteristic structure, is present in all the Ischnocera, and seems to have an important function in grasping the feather and directing it towards the mandibles for attachment and feeding. Posteriorly the mandibular framework is prolonged backwards and may or may not reach the occipital margin. The various modifications which have taken place in this primitive type of head together with a terminology for those parts of importance in classification follows :

Preantennal Region.

Marginal carina (epistoma, Kéler, 1938 ; frontal band, Harrison, 1937).—In the primitive forms, as already shown, this band forms the rim of the preantennal region (fig. 10) ; in some genera (*Episbates*) there may be no definite thickening round the anterior margin of the head. This carina turns inwards immediately anterior to the antenna each side to form the thickened preantennal nodus dorsally, and to fuse with the articulation of the mandibles ventrally. Dorsally the thickening may pass inwards from the nodus to form the transverse carina, either interrupted medianly (*Saemundssonina*, fig. 11) or continuous across the head (*Columbicola*). The primitive form of the marginal carina may become modified in the following ways :

1. In the mid-part of the anterior margin the carina may become depressed to a greater or less extent ; at the place of this depression the anterior margin of the head is hyaline (the hyaline margin). Example : *Brüelia brachythorax* fig. 19.

2. The marginal carina may be divided into two or more parts by interruptions of its sclerotization as follows :

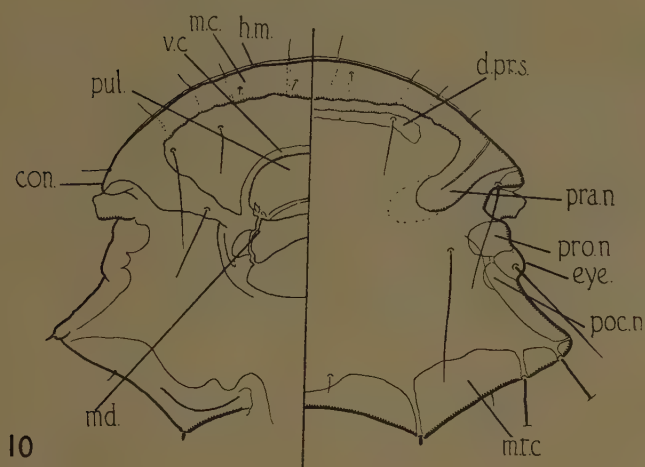
A median interruption in the anterior part of the carina giving a marginal carina each side of the head. Example : *Aptericola* (fig. 12, *m. c.*).

A lateral interruption each side giving a postmarginal carina (antennal band Piaget, 1885) running from the preantennal nodus to the interruption, and the premarginal carina (clypeal band, Piaget, 1885) running from the lateral interruption to the median anterior interruption (fig. 11, *pom. c.* and *prm. c.*).

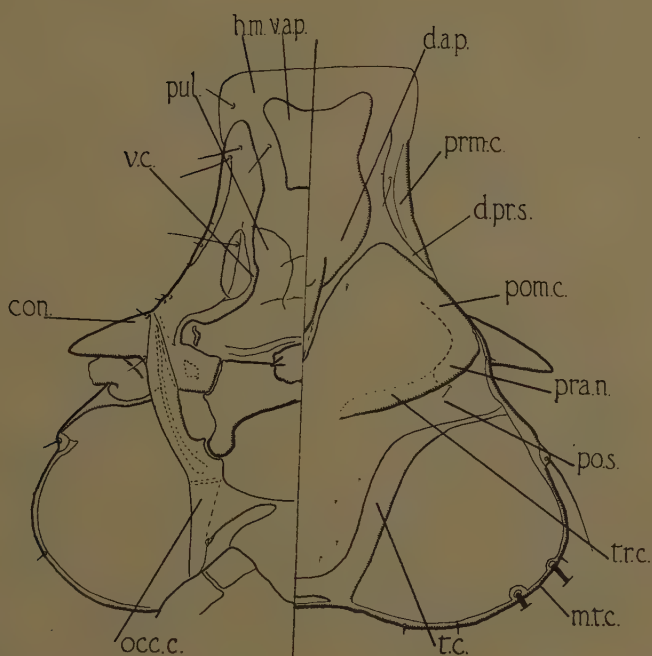
In some species the marginal carina may be interrupted medianly and continued forward as the hyaline margin dorsally, but ventrally shows a further pigmented and sclerotized portion which fuses with the prolonged ventral carina. Example : *Meropoecus*, *Rallicola* species.

The dorsal preantennal suture and the anterior plate (clypeal signature, auctorum).—The dorsal surface of the preantennal region may have a suture

¹ Kéler has given a full account of the morphology of two Ischnoceran heads (1938 and 1939), so that details of the structures need not be repeated.



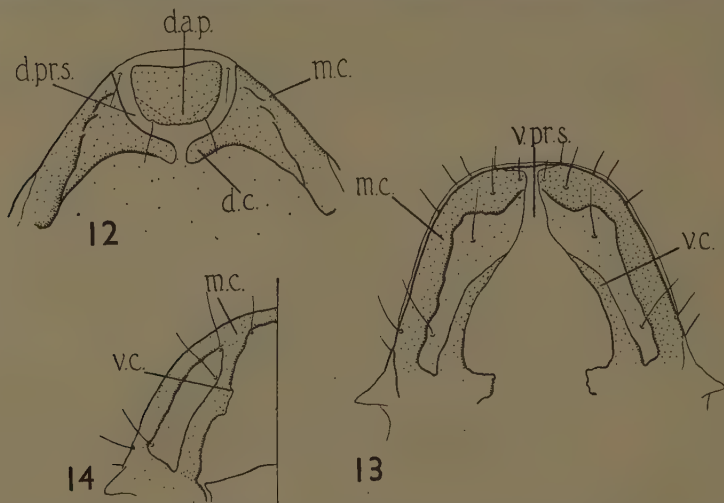
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11

FIGS. 10, 11.—(10) *Goniodes* sp., head. (11) *Saemundssonina* sp., head. con, Conus; d.a.p., dorsal anterior plate; d.p.s., dorsal preantennal suture; h.m., hyaline margin; m.c., marginal carina; md., mandible; m.t.c., marginal temporal carina; occ.c., occipital carina; poc.n., postocular nodus; pom.c., postmarginial carina; pos., postantennal suture; pran., preantennal nodus; prm.c., premarginial carina; pron., preocular nodus; pul., pulvinus; t.c., temporal carina; tr.c., transverse carina; v.a.p., ventral anterior plate; v.c., ventral carina.

which either does not reach the marginal carina (some species of *Goniodes*, fig. 10, *d.pr.s.*), or reaches but does not interrupt it. A suture such as is found in *Lagopoecus* cuts off a semicircular area of the dorsal surface; if the marginal carina is now interrupted medianly a distinct area of the dorsal surface will be cut off, forming the so-called "clypeal signature" (here called the dorsal anterior plate), a characteristic feature of many Ischnoceran heads. The anterior plate also has a ventral component (ventral anterior plate, fig. 11, *v.a.p.*) which may be fused to the dorsal plate throughout its length, and thus forms a solid block of sclerotization throughout the depth of the head as in *Brüelia marginalis* (fig. 6), or it may be fused only at its proximal end as in *Philopterus* (figs. 7 and 9). The ventral plate may be a narrow rim across the anterior part of the anterior plate as in *Haliperus*, where it is striated, or it



FIGS. 12-14.—Preantennal region of heads. (12) *Apterocola* sp., dorsal. (13) *Degeeriella* sp., ventral. (14) *Tinamotaecola* sp., ventral. *d.c.*, Dorsal carina; *v.pr.s.*, ventral preantennal suture; explanation of other letters as in figs. 10, 11.

may be longer, narrowing proximally, and with a flattened, rounded or pointed proximal margin (fig. 11). It seems possible that the ventral plate in some genera represents the median portion of the marginal carina which has been cut off by sutures from the lateral part of the carina each side. In its simplest form the dorsal anterior plate is merely an area of the dorsal surface of the head cut off by a suture (*Rallicola*, *Brüelia*), but it may become modified by internal thickening, and in some genera has a single (*Saemundssonina*, *Philopterus*) or double (*Ibidocetus*) heavily sclerotized backwardly directed point.

The dorsal preantennal suture, which cuts off the anterior plate posteriorly, arises in the more modified forms either at the distal ends of the interrupted marginal carinae (*Apterocola*, fig. 12, *Meropoecus*), or at the distal ends of the postmarginal carinae (*Saemundssonina*, fig. 11, *Philopterus*, *Quadriceps*). In some genera the dorsal suture is not continued across the head and is represented by two lateral sutures each side of the dorsal plate, the posterior part of this plate thus being continuous with the rest of the dorsal surface

of the head (*Brüelia* species and *Craspedonirmus*). Some adults which show no dorsal suture have nymphs in which a dorsal suture is present (with which the anterior dorsal setae (see below) are associated). It is possible, therefore, that the adult suture represents part of this nymphal suture and that its absence in some adults is secondary. This also applies to the postantennal suture.

The proximal edge of the dorsal suture may have a line of thickening (fig. 12, *d.c.*)—the dorsal carina (internal bands, Harrison, 1937). This thickening may be continuous across the head (*Pseudonirmus*), or turned posteriorly in the midline and prolonged as two parallel bands. In *Halipeurus* the ends of these two bands actually lie free in the head cavity. Other parts of the dorsal surface of the preantennal region may have various areas of thickening, either proximal to the dorsal suture (some species of *Columbicola*), or anteriorly where there is no dorsal suture.

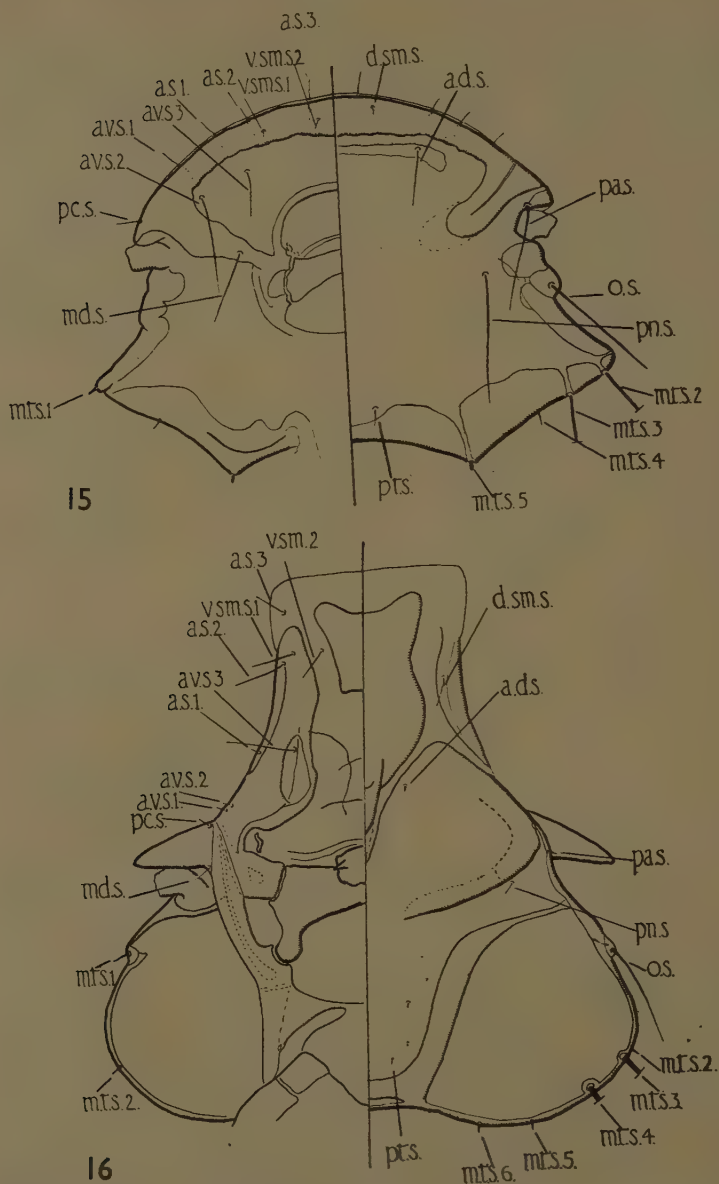
The pulvinus and ventral carina (Zygoma, Kéler, 1938; ventral bands, Harrison, 1937; internal bands, Piaget, 1885).—The ventral carina is continuous with the marginal carina and the mandibular framework, and is the thickening to which the pulvinus is attached. This latter structure, as already mentioned, is of importance in feeding and attachment, and the form of the ventral carina seems to be closely correlated with that of the pulvinus. In *Lipeurus* the pulvinus is a simple lobe attached to the complete semicircular ventral carina (fig. 8), and similarly in *Perineus* (Plate I, fig. 1), although in this genus there is no definite carina medianly. In *Coloceras* (Plate I, fig. 2), in which the ventral carina is complete, the pulvinus has a lateral lobe each side, giving a broad median groove (the mouth-channel, Kéler, 1938: 403). In the most highly modified forms, where the ventral carina is interrupted medianly and each carina has a thickened flattened surface lying parallel to the one on the other side, the pulvinus has a well-developed lateral lobe each side attached to this parallel part of the ventral carina (Plate I, fig. 4). In these forms the piece of feather being eaten lies in a central groove, held in position by the lateral lobes, and the pulvinus thus forms an efficient holding organ. The central portion of the pulvinus is also extrusible, and may be blown out as a lobe like structure (fig. 5, *pul.*). In such forms as *Philoceanus becki* and *Trabeculus* the pulvinus reaches its greatest development and has caused distortion of the preantennal region: in the latter genus the ventral carinae are pushed outwards proximally, where they fuse with the marginal carina. The surface of the pulvinus may be smooth or slightly sculptured and in some genera (*Austrogoniodes*, *Anaticola*, Plate I, fig. 3) the central groove has a median line of sclerotization.

The ventral carina, which in the more primitive forms passes forward from the mandibular framework each side to form a complete semicircle (Plate I, fig. 2 and fig. 10), may be modified in the following ways:

It may be interrupted medianly so that the thickening is only visible laterally, the pulvinus being attached to the edge of the sclerotized surface of the mid preantennal region. Example: *Episbates*.

It may be interrupted medianly with a suture—the ventral preantennal suture—running forwards from the two ends of the carina to, or nearly to, the complete marginal carina. Example: *Degeeriella* (fig. 13).

The edge of the ventral preantennal suture may be thickened each side (thus becoming a continuation of the ventral carina), and fused distally with the complete marginal carina. Example: *Tinamotaecola* (fig. 14).



FIGS. 15, 16.—Heads to show setae. (15) *Goniodes* sp. (16) *Saemundssonina* sp. *a.d.s.*, anterior dorsal seta; *a.s.*, anterior seta; *a.v.s.*, anterior ventral seta; *d.sm.s.*, dorsal submarginal seta; *md.s.*, mandibular seta; *mt.s.*, marginal temporal seta; *o.s.*, ocular seta; *pa.s.*, preantennal seta; *pc.s.*, preconal seta; *pn.s.*, postnodal seta; *pt.s.*, posttemporal seta; *v.sm.s.*, ventral submarginal seta.

Part of the ventral carina each side may form a thickened flattened surface, lying parallel to that of the opposite side, to which the lobes of the pulvinus are attached. The ventral carinae may or may not reach the complete marginal carina, or the marginal carina may be interrupted medianly and the ventral carina fused to its edge each side (Plate I, fig. 4). In many genera the ventral carina does not form a distinct band anteriorly as in *Tinamotaecola* (fig. 14), but has a thickened inner edge only. Example: *Saemundssonina* (fig. 11).

In the more specialized heads the area between the proximal part of the ventral carina and the marginal carina has various modifications which may form useful generic characters.

In some of the genera (e.g., *Halipeurus*) parasitizing the Procellariiformes there is a line of demarcation running anteriorly from the interrupted ventral carinae each side, giving a similar appearance to a ventral preantennal suture, but the surface of this area is sclerotized and sculptured (possibly secondarily). In *Halipeurus* and other genera from the Procellariiformes the ventral carinae merge with the inner ventral surface of the head shortly after their proximal point of origin, but distally there is an isolated band of thickening along each side of the line of demarcation, which may be called the ventral carina. Another modification found in one of the genera (*Naubates*) from the Procellariiformes is the presence of a more dorsal posterior prolongation of the ventral carina, which probably gives some extra support to the pulvinus.

As the preantennal region becomes more modified the ventral carinae become thicker and the attachment of the pulvinus more specialized. A comparison of fig. 4 (*Coloceras*) and fig. 5 (*Philopterus*) demonstrates this increase in complexity of the pulvinus and ventral carinae.

Postantennal Region.

Temporal carina (temple band, of some authors; occipital band, Piaget, 1885; zügel, Kéler, 1938).—This endocarina, when present, runs from the occipital margin of the head across the temples, and becomes continuous either with the preantennal nodus (*Philopterus*, *Cummingsiella*), or with the temple margin just above the eye (*Saemundssonina*, fig. 11, *t.c.*). In many species it merges with the inner surface of the dorsal sclerotization, and is only apparent near its point of origin at the occipital margin.

Marginal temporal carina.—The temples are usually enclosed by a thickened rim—the marginal temporal carina, which may be enlarged into irregularly shaped patches of thickening round the eye—the preocular nodus and the postocular nodus—and on the occipital margin—the occipital nodus.

The postantennal suture.—This suture either passes across the temples (*Lagopoecus*) or appears as two lateral sutures (*Quadriceps*).

The occipital carina (tremse, Kéler, 1948).—This runs backwards each side from the mandibular framework and may or may not fuse with the occipital margin; the posterior tentorial pits are always associated with this occipital thickening.

The chaetotaxy.

The setae of the head are remarkably constant in position and number throughout the Ischnocera, and can frequently be used as guides to certain parts of the head. There are five pairs of setae which are always present and approximately in the same position throughout the superfamily; these are:

A ventral seta arising just anterior to the conus—the preconal seta (*pc.s.*, figs. 15 and 16).

A ventral seta, on, or near the outer surface of the mandibular framework, the mandibular seta (*md.s.*). In some species (e.g., *Pectinopygus* sp.) this seta has become pushed out laterally and actually arises on the lower margin of the conus.

A seta on the dorsal, usually anterior, edge of the antennal socket, the preantennal seta (*pa.s.*).

A dorsal seta posterior to the preantennal nodus, the postnodal seta (*pn.s.*). Where there is a postantennal dorsal suture this seta lies in or near the suture (fig. 16, *pn.s.*).

A seta arising on the dorsal surface of the lens of the eye, the ocular seta (*o.s.*).

The remaining setae are also found throughout the superfamily, but their position, and sometimes number, is not so constant. In the primitive type of head (e.g., *Goniodes*, fig. 15) there are four or five setae arising on the anterior margin each side of the midline; in other genera (e.g., *Trogoninirmus*), also with a complete marginal carina (or circumfasciate head), they may originate submarginally on the dorsal surface. In the modified type of head (fig. 16) the outer of these marginal setae is associated with one of the anterior ventral setae (see below), and is here called the first anterior ventral setae (*a.v.s.* 1). As the remaining three or four may be marginal or submarginal on the dorsal or ventral surface they are called the anterior setae (*a.s.* 1-3).²

Where the dorsal preantennal suture interrupts the marginal carina the first anterior seta is often (but not invariably) associated with the point of interruption, either marginally or submarginally on the dorsal or more rarely on the ventral surface. In those species where the dorsal suture does not interrupt the marginal carina though they belong to a genus in which the majority of species show the interruption, as in *Philopterus*, then the first anterior seta will be found at the lateral edge of the dorsal suture, that is, near the point where the interruption of the marginal carina usually occurs in species of *Philopterus*.

Arising on the ventral surface of the marginal carina in the primitive type of head, each side of and near the midline is a pair of setae—the ventral submarginal setae (*v.sm.s.* 1-2). In other genera (e.g., *Lipeurus*, *Degeeriella*, *Labicotes*, *Otidoecus*) these may arise on the ventral surface below the marginal carina. In the most specialized type of head (fig. 16) the outer of this pair (*v.sm.s.* 1) usually lies on the marginal carina and the inner (*v.sm.s.* 2) just lateral to the ventral anterior plate. In *Anatoecus* this latter seta is minute and difficult to see.

Lateral and posterior to the ventral submarginal setae are two ventral setae each side—the anterior ventral setae (*a.v.s.* 2-3). In specialized forms where the ventral carina is modified these two setae, together with the first of the marginal setae (*a.v.s.* 1), often form a characteristic group associated with the ventral carina and the area between it and the lateral margin of the head—these three setae are called the anterior ventral setae (*a.v.s.* 1-3). In some genera (e.g., *Philopterus*, *Saemundssonina*, *Degeeriella*) the outer two (*a.v.s.* 1-2) are close together and arise just anterior to the preconal seta; in others (e.g., *Naubates*, *Halipeurus*, *Anaticola*, some species of *Pectinopygus*) all the

² All setae are counted from the lateral margins of the head towards the midline, and those on each half of the head are counted separately.

anterior ventral setae may be grouped much nearer the front of the head, or (e.g., *Degeeriella*, *Rhynonirmus*) *a.v.s.* 1-2 may arise near the conus and *a.v.s.* 3 near the anterior margin of the head. Their position seems to be mainly dependent on the shape of the head.

On the dorsal surface of the preantennal region there is a single submarginal seta lying each side of the midline, either on the marginal carina or just below it—the dorsal submarginal seta (*d.sm.s.*). In the specialized forms this is usually found on the premarginal carina (fig. 16, *d.sm.s.*). Posterior to this seta is a single seta—the anterior dorsal seta (*a.d.s.*), which is commonly associated with the dorsal preantennal suture when this is present. In the great majority of species with modified heads this seta arises either in the suture or on its posterior margin. However, in some genera (e.g., *Haliperus*) it may arise some distance posterior to the suture, or its position in relation to the suture may vary in different species of one genus (e.g., *Ardeicola*). In *Columbicola* the anterior dorsal setae are never associated with the suture (which in any case may not be homologous with the dorsal suture of other genera), and there is a second pair of setae posterior to these, about the level of the conus.

The margins of the temple always have a number of setae, some arising dorsally and some ventrally, but for the purposes of terminology they are all called the marginal temporal setae (*m.t.s.* 1, 2, 3 . . .). The first seta on the temple (*m.t.s.* 1) usually arises on the ventral surface just behind the eye; in a few genera (e.g., *Saemundssonina*) it is actually on the ventral surface of the lens, and in others (e.g., species of *Goniodes*) it may arise some considerable distance behind the eye. Its position on the eye is apparently of generic value in *Saemundssonina*. Specimens of this genus have been examined from 52 species belonging to 24 genera of the Charadrii, 39 species belonging to 11 genera of the Lari, 8 species of 5 genera of Alcae, 8 species of 8 genera of Procellariiformes and 1 species of GRUIDAE. In all these the first marginal temporal seta is on the lens. In *Quadriceps*, probably a related genus, this seta may be either on the lens or just below it, and where it is close to the lens it arises on it in some specimens of a species and below it in others. The remaining temporal setae usually comprise a small ventral seta (*m.t.s.* 2), two dorsal macrochaetae, and two smaller setae on the occipital margin (fig. 16). But there is considerable variation in the number and size of the temporal setae even within one genus: in *Goniodes* many of the species have the number as shown in fig. 15, but *G. wilsoni* and *G. perlatus* have eight or more elongated setae each side.

Near the midline on each side there is a single seta above the occipital margin, the post-temporal seta (*pt.s.*).

All or any of the head setae may become greatly elongate (e.g., *Meinertzhageniella*) or reduced to stout spines (e.g., *Austrophilopterus*, *Anatoecus*), or reduced to microchaeta so that they are often difficult to find. Some species may have additional setae on the dorsal surface of the head (e.g., *Austrogoniodes*), arranged in such a way that it is no longer possible to identify the primitive ones to which names have been given. Abnormally any of the setae may be duplicated in a specimen, often on one side of the head only.

The Phylogenetic Importance of the Characters of the Head.

In the superfamily Amblycera (which is the more primitive) the mandibles are near the anterior margin of the head; in the Ischnocera the region of the

head in front of the mandibles has become elongated, sometimes to a considerable extent in the more specialized genera such as *Craspedorrhynchus* and *Echinophilopterus*. With the elongation of the preantennal region is found the tendency for the breakdown of its rigidity by the formation of sutures and by the interruptions of the endocarinae. The most important line of evolution seems to have been that which increased the efficiency of the pulvinus as a holding groove for pieces of feathers. This was achieved by the interruption of the primitive semicircular ventral carina, thus increasing the mobility of the pulvinus and giving better attachment for its lateral lobes. This interruption of the ventral carina has certainly taken place more than once—the HEPTAPSOGASTRIDAE have genera both with and without the complete carina. The prolongation of the ventral carina each side and its fusion with the interrupted marginal carinae gives additional support to the pulvinus, and strengthens that form of head in which the presence of both dorsal and ventral membranous areas allows a limited mobility. Although the interruption of the endocarinae and the formation of sutures have probably taken place on the same general lines in unrelated stocks, their present arrangement differs in detail to a greater or less extent. These differences may have been caused by the differences in the minute feather structure of the host. There are only four host groups—the Sphenisciformes, Tinamiformes, the Galli and the COLUMBAE on which the parasite genera with unmodified heads are dominant; the last three groups also have parasite genera with modified heads. On the Tinamiformes are found *Pseudolipeurus*, *Pseudophilopterus*, and *Tinamotaecola*, all with modified heads, and even within the family HEPTAPSOGASTRIDAE the ventral carina is interrupted in some genera (e.g., *Megapeostus*) and the marginal carina modified (e.g., *Discocorpus*). In the genera from the Galli, apart from *Lagopoeus* and *Cuculotogaster* in which the ventral carina is interrupted, *Oxylipeurus* shows a tendency towards the formation of anterior sutures and the modifications of the marginal carina. In *Columbicola* from the COLUMBAE the ventral carina is interrupted and the anterior region of the head shows considerable modification. One genus (*Episbates*) on the Procellariiformes has the head unmodified, but all the other genera from this Order and the rest of the Aves have the head modified in some way even if it is only the median interruption of the ventral carina. It would seem, therefore, that the modifications of the preantennal region of the head are advantageous to the parasites on the majority of bird orders. Elsewhere (Clay, *in press*) tentative suggestions have been made on the possible role played by the minute structure of the feathers in the retention of the primitive features of the head.

Brüelia, a genus which parasitizes the Passeriformes and some related orders, comprises a large number of species, amongst which can be traced a series from those with an entire marginal carina and no anterior plate, to those with the marginal carina interrupted medianly and laterally, and with the anterior plate well developed. Thus, the species from *Podoces* (fig. 17) shows the complete marginal carina although medianly less heavily sclerotized, that from *Nucifraga* (fig. 18) shows a greater median modification, that from *Bombycilla* (fig. 19), the types species of *Brüelia*, has the marginal carina indented medianly and the anterior margin of the head at this point hyaline. In this and other species there is a triangular-shaped area of sclerotization in the indented part of the marginal carina. In the species (fig. 20) from *Harpactes erythrocephalus* (Trogoniformes) the marginal carina is entire, but

there is a dorsal suture which cuts off a simple anterior plate. In that from *Turdus pilaris* (fig. 21) the marginal carina is interrupted medianly and there is an incomplete interruption laterally; the dorsal suture does not pass across the head, and leaves the posterior part of the anterior plate continuous with the dorsal sclerotization of the head. In the species from *Turdus merula*, *Brüelia merulensis* (fig. 22), the marginal carina is interrupted medianly and laterally and there is a well-marked dorsal suture and anterior plate. The nymph of this latter species (fig. 23) has the marginal carina entire, and similar to that of the adults of other species of *Brüelia*.

Ventrally all species of *Brüelia* have the ventral carina interrupted. In some the ventral carina may be sclerotized only proximally each side (species from *Podoces*, fig. 24), giving a situation similar to that in *Degeeriella* (fig. 13). In those species in which the marginal carina is complete (but indented) dorsally and interrupted ventrally, the sclerotization of the inner edge of the ventral carina is carried forward each side to fuse with the interrupted marginal carina; in *Brüelia merulensis*, where the marginal carina is divided laterally into a pre- and postmarginal portion, this sclerotization is fused to the distal ends of the premarginal carinae (fig. 25). *Sturnidoecus*, obviously nearly related to *Brüelia*, owes its distinctive appearance to the elongation of this ventral thickening beyond the dorsal marginal carina, and to its broader head, which has those characters associated with increased size (see below). Thus, the species of *Brüelia*, which by the characters of the abdomen form a compact group, show considerable diversity in the characters of the head. Any attempt to separate them into genera on these head characters would mean the erection of five or six genera, which would not only grade into each other but completely obscure their relationships, and in some cases would mean the association of a number of species not forming a natural group. The characters on which *Guimaraesiella* Eichler, 1949, for instance, was separated from *Brüelia* are found not only in the type-species, *Docophorus subalbicans* from the PARADISEIDAE, but in species from the TURDIDAE, GEOSPIZIDAE and others. There seems no reason, therefore, to recognize the following genera: *Corvonirmus* Eichler, *Guimaraesiella* Eichler, *Xobugirado* Eichler, *Meropsiella* Conci, *Painjunirmus* Ansari and *Traihoriella* Ansari. The genera *Sturnidoecus* and *Bizarriifrons* and species from the CORACIDAE (" *Docophorus* " *longipes* Piaget) are also closely related to *Brüelia*, as shown by the characters of the abdomen, but have probably diverged far enough from their original *Brüelia*-like ancestor to be recognized generically.

The most specialized species of *Brüelia* (for example, *B. merulensis* or *B. galapagensis*) have a form of head which, with various minor modifications, is found in a great number of related or not closely related forms. The characters of this head are as follows:

Part of the median anterior margin of the head hyaline.

Marginal carina interrupted anteriorly and laterally.

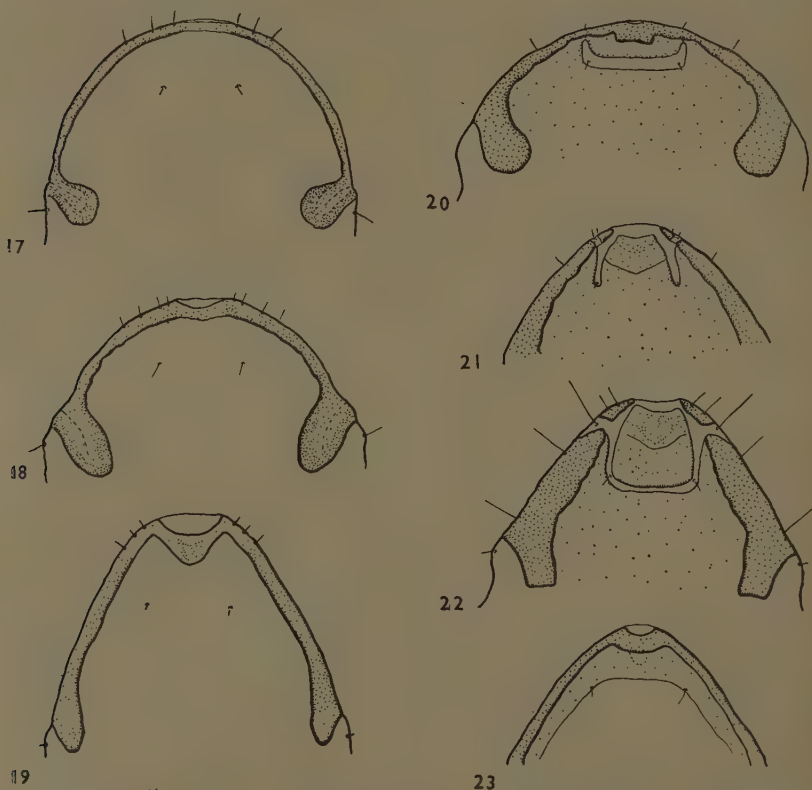
Dorsal preantennal suture and dorsal and ventral anterior plate present.

Ventral carina interrupted and fused to the ends of the premarginal carina.

Pulvinus with lobes attached to the flattened parallel surfaces of the ventral carina.

In those species with heads modified on the above lines some show the complete marginal carina (at least dorsally) in the nymph, for example

Brüelia merulensis (fig. 23), *Strigiphilus oculatus* (fig. 26), *Aptericola novae-zealandiae*; in others such as *Philopterus* even the first stage nymphs are little different from the adult. This may mean that either the latter have been established for a longer period of time, or (which is more likely) they have assumed a mode of life which necessitates the modification of the head and without which the nymphs could not survive. It is probable that this type of head has been evolved more than once in both related and unrelated

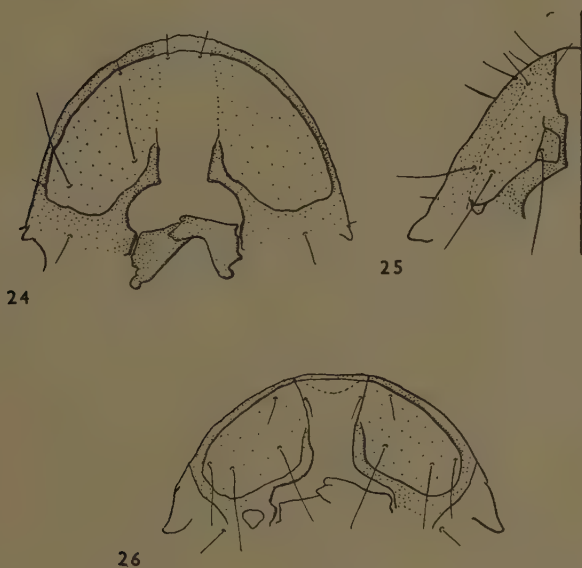


FIGS. 17-23.—Preantennal region of the head, dorsal. (17) *Brüelia koslovae*. (18) *B. multipunctata*. (19) *B. brachythorax*. (20) *Brüelia* species from *Harpactes erythrocephalus*. (21) *B. marginata*. (22) *B. merulensis*. (23) *B. merulensis*, nymph.

forms, due no doubt to the similarity of the basic Ischnoceran type in which specialization would be forced to take place on similar lines (see Clay, 1949, for fuller discussion). Thus, *Philopterus*, *Quadriceps*, *Wilseniella*, *Multicola*, *Penenirmus* and *Pectinopygus* all have this general type of head, but are in no way closely related. It is not supposed that all the genera with this similar type of head evolved on the same lines, nor that the development from nymph to adult is always the same—an examination of the nymphs of *Ibidoecus*, for instance, suggests that the anterior plate has been formed rather differently

from that of *Brüelia*. It is possible that the method of formation of the dorsal suture and anterior plate may give an indication of relationships between the genera, but a study of the embryology and nymphal development will have to be made before a supra-generic classification based on mode of development can be formulated.

Although this form of modification of the head (discussed above) appears to be the most widespread, examples being found on the majority of bird orders, there are cases where specialization has been achieved on other lines. The genera of Ischnocera found on the Galli have the primitive type of head with a complete marginal carina and uninterrupted ventral carina (fig. 10), or if interrupted the sclerotization is not carried forward. One genus, *Oxylipeurus*, however, shows a tendency for the anterior region of the head to become



FIGS. 24-26.—Preantennal region of the head, ventral. (24) *Brüelia koslovae*. (25) *B. merulensis*. (26) *Strigiphilus oculatus*, nymph.

modified in various ways. The unmodified species (e.g., *O. mesopelios*) have a complete marginal carina with the dorsal preantennal suture not interrupting the marginal carina laterally; the dorsal suture may be indistinct (species from *Oreortyx*, *Epicolinus* Carriker), or absent (*O. himalayensis* from *Tragopan* and a species from *Crax*). In other species (e.g., *O. repandus*) the preantennal suture may partially interrupt the marginal carina laterally; in *O. inaequalis* the postero-lateral margin of the suture is sclerotized each side, giving short dorsal carinae. In *O. megalops* there is considerable modification of the anterior part of the head in a way which cannot be homologized with that discussed under *Brüelia*, and which is unlikely to lead to a form of head found in the most specialized species of that genus, although it is a type which could have led to the modifications found in *Columbicola*. The

temporal carinae are never fully developed, and may be absent. The pulvinus is either of the primitive lobe-like type, or has lateral lobes as in *Coloceras*, or internal sclerotization (*O. ischnocephalus*). The ventral carina usually merges each side with the ventral sclerotization of the head, and does not join with that of the other side to form a definite semicircular band as in *Goniodes* (fig. 10). The sclerotization may be interrupted by a ventral suture which runs anteriorly (as in *Degeeriella*), reaching nearly to the marginal carina (*O. megalops*); in *O. aepypodius* there is a thickening along the edges of part of this suture forming distally short ventral carinae similar to those found in *Pseudonitmus*.

Thus *Oxylipeurus*, parasitizing a single host order, comprises a related group of species (as shown by the characters of the abdomen) which show a tendency towards the modification of the anterior region of the head. This has probably taken place more than once, sometimes on parallel lines, in different groups of species restricted to particular families of birds. It seems unsatisfactory to use these head characters as criteria for the erection of genera—at least six of such genera would be needed, and in some cases would include species from unrelated host groups. The two genera already separated from *Oxylipeurus*, namely *Eiconolipeurus* and *Epicolinus*, should, therefore, not be recognized; *Splendoroffula*, found on the MUSOPHAGIDAE, is also doubtfully separable from *Oxylipeurus*.

Structural modifications in the Ischnocera have been caused by the adaptation of the parasite to the environment of the different ecological niches on the body of the bird. This factor has been discussed elsewhere (Clay, 1949), but in relation to the structure of the head it was the occupation of the head and neck niche which seems to have had the most important influence. The occupants of this niche have a broader head, correlated with the general shortening and broadening of the whole body. This enlargement of the head is usually associated with the prolongation of the head anteriorly and with the enlargement of the mandibles and the concomitant development of the mandibular framework. This type of head shows the greatest development of endocarinae, presumably for support of the larger mandibles and the larger size of the head in general. It also has the greatest development of sutures in the preantennal region, possibly to give a limited mobility to this flattened expansion of the head. In the postantennal region support is given to the mandibular framework by the prolongation of the occipital carinae to the occipital margin; and further support to this region is given by the development of the temporal carinae. Although well developed temporal carinae are found in narrow-headed forms, these lines of thickening are, in general, characteristic of the broad-headed forms, and are found in such unrelated genera as *Megaginus*, *Docophoroides*, *Trabeculus*, *Anatocetus*, *Philopterus* and *Sturnidoecus*. Moreover, where there are two related genera or species groups which differ mainly in shape, these endocarinae are usually present in the broad-headed forms and absent in the narrow-headed ones: thus *Sturnidoecus* has these carinae well developed, unlike *Brüelia*, in which the species have narrower heads; *Acutifrons* contains broad-headed species, which differ only from *Degeeriella* by the well-developed temporal carinae; *Cuculicola cheluria*, a broad-headed species, has well-developed temporal carinae, which are absent in the narrow-headed *Cuculicola latirostris*.

Thus, the apparent similarity between different genera is often caused by linked characters dependent on the environment in which the parasite lives;

this has resulted in many of the round-bodied, large-headed forms (head lice) being placed in one family and many of the long-bodied narrow forms (wing lice) in another. On the other hand, it has also led to the erection of genera for groups of species which, because they have changed their habitat or possibly because their host has a broader type of feather with the resulting broadening of the parasite, differ only in those superficial characters of the head (and sometimes abdomen) correlated with increased size. It is doubtful, for instance, whether *Acutifrons* is more than a species group of *Degeeriella*. Hopkins (1943), in a most instructive paper, has shown how the TRICHO-DECTIDAE from the antelopes have been separated into genera on adaptive, not phylogenetic characters, the environmental factor probably responsible being the texture of the coat of the host.

The value of the characters of the head in showing phylogenetic relationships can now be summarized. The variation is discussed in relation to characters of the abdomen which are constant throughout any group in question.

Marginal carina.—In many groups the form of this carina is a good generic character, but there are a number of exceptions: *Brüelia* and *Oxylipeurus* have already been discussed; in *Philopterus* the marginal carina may have the well-marked lateral interruption characteristic of most of the genus, or there may be no interruption but a deep indentation (species from *Megarhynchus*, TYRANNIDAE), or the marginal carinae may be complete laterally (species from the PITIIDAE). Although the form of the marginal carina may sometimes be a generic character, there seems little doubt that it will not form a supra-generic character except in those cases where it is unmodified (GONIODIDAE); the majority of families will probably prove to have genera with the carinae both entire and specialized to a greater or less extent.

Hyaline margin.—This region is only appreciably developed in those forms with modified heads, although it seems to be homologous with the narrow hyaline rim of the head in *Goniodes* (fig. 10) called the "limbus" by Kéler (1939: 14). Its form is largely dependent on that of the marginal carina and, therefore, in a genus (e.g., *Brüelia*) where there is considerable variation of this carina there is also variation of the hyaline margin. In *Ralliola*, where it is always present, it may be extremely narrow (*R. fulicae*) or broad (*R. ortygometrae*). In those species with modified heads its point of origin each side gives a characteristic appearance. In *Anatoecus*, *Craspedonirmus* and *Carduiceps* it arises each side at the point of the lateral interruption of the marginal carina, and this point of origin appears to be constant and characteristic throughout these genera. In other genera its point of origin varies: in *Philopterus*, for instance, it may arise at the anterior ends of the marginal carinae (*P. cincli*), or some little way proximal to this (species from *Graculus*); its breadth at the lateral sides of the head also varies in this genus: it may run forward as a narrow strip (*P. fringillae*), or be enlarged laterally (species from *Dicrurus*, MOMOTIDAE and others), giving a characteristic appearance to the head. The anterior edge of the hyaline margin may be medianly indented as a generic character (*Incidifrons*), or as a specific character (*Philopterus*); the anterior edge may be more heavily sclerotized and pigmented, a character found in some species of *Philopterus* (those from the MOMOTIDAE, TYRANNIDAE, NECTARINIDAE and others) and in the species of *Penenirmus* parasitizing the CAPITONIDAE (Barbets).

Dorsal carina.—The form of this carina (bordering the posterior edge of the preantennal suture) may be of generic value (*Pseudonirmus*), or vary

considerably in closely related forms: in the *Saemundssonina* species from *Alle alle* it is strongly developed and passes round the posterior end of the preantennal suture, while in the species from another of the ALCIDAE (*Fratercula arctica*) it is scarcely developed.

Transverse carina.—Where this is present as a complete band across the head it seems to be constant throughout the genus (e.g., *Columbicola*), but it is not of supra-generic importance, as in *Turturicola*, apparently related to *Columbicola*, it is absent.

Temporal carina.—These carinae may be absent, partially developed or fully developed within one genus, but their distal point of termination when fully developed seems to be constant throughout a genus; in *Philopterus*, for instance, they pass to the preantennal nodus, and in *Saemundssonina* to the preocular nodus.

Anterior plate.—In those genera containing species in which the dorsal anterior plate is a superficial area marked off from the rest of the preantennal surface of the head by the dorsal suture, there may also be species where it is absent altogether (e.g., *Brüelia*). Where the anterior plate is a thickened discrete structure its form is usually of generic value (e.g., *Ibidoecus*). There are, however, exceptions: in the *Philopterus* species from the PITIDAE the posterior prolongation of the anterior plate is lightly sclerotized, and is not the heavily thickened point characteristic of most species of *Philopterus*; in one species of *Quadriceps* (from *Limnodromas griseus*) the posterior part of the plate is prolonged into a thickened point, and is similar to that found in *Saemundssonina*.

Dorsal suture.—Where the marginal carina is complete the presence or absence of a dorsal suture (e.g., *Goniodes*, *Lagopoecus*) is rarely a generic character. Again in the same genus it may or may not be continued to the margin and interrupt the marginal carina (*Oxylipeurus*, *Brüelia*). In the forms with specialized heads where it is present throughout the genus, its point of origin is usually constant: in *Rallicola* (species examined from 23 genera of RALLIDAE) the marginal carina is never interrupted laterally, and the dorsal suture always arises at the anterior end of the marginal carina each side; and in *Philopterus*, even in those species where the marginal carinae is not interrupted, the dorsal suture always arises near the middle of the preantennal region. In the species with modified heads the form of the dorsal suture also seems to be generically constant: either passing straight across the head (*Luniceps*), passing posteriorly to a point (*Quadriceps*) or as two points (*Sturmiidoecus*).

Ventral carina.—This endocarina shows great diversity throughout the Ischnocera, and its form is rarely (perhaps in the GONTODIDAE) a supra-generic character. It may be entire or interrupted in the same genus (*Heptapso-gaster*), but its general form tends to be constant throughout a group of related species. In *Brüelia*, for instance, in which there is much diversity of head form, the ventral carina is always interrupted and the sclerotization carried forward as a flattened surface each side (fig. 24); in *Degeeriella* (fig. 13), in which the general form of the head resembles that of the simplest species of *Brüelia*, the ventral carina is always interrupted, but the sclerotization is not carried forward in the form found in *Brüelia*. The ventral carinae may or may not be fused with the marginal band within one genus (*Brüelia*). The area between the proximal part of the ventral and marginal carinae may show generic characters in the specialized forms (e.g., *Saemundssonina*). The form

of the pulvinus is closely linked with that of the ventral carina, and its character seems to be constant through groups of related species.

Occipital carina.—These may or may not reach the occiput in the same genus (e.g., *Oxylipeurus*).

Gular plate.—A true gular plate seems to be absent in all the GONIODIDAE, *Austrogoniodes*, *Chelopistes*, some of the genera of the HEPTAPSOGASTRIDAE and in some of the genera parasitizing the Procellariiformes. In *Oxylipeurus* it may or may not be present. In *Colilipeurus* and *Turnicola* it is apparently absent, but may only lack pigmentation. It is also absent in *Hopkinsiella*, although in related genera it is present. The presence of a gular plate may, therefore, be a supra-generic, generic, or only a specific character.

Antennae and conus.—These structures have already been discussed (Clay, 1946: 355) and it was suggested that the form of the conus was often correlated with the size of the antennae, and that sexual dimorphism in either of these structures was of little phylogenetic interest, the presence or absence of sexual dimorphism being found in closely related species. In *Philopterus* the conus may be well developed (species from CAMPEPHAGIDAE), reduced (species from TYRANNIDAE), or absent (species from PITTIDAE).

Chaetotaxy.—As already shown, the setae are, in general, constant throughout the Ischnocera and do not show supra-generic characters. The form of the setae may be of generic value: the spine-like dorsal setae of *Anatoecus*, the peculiar flattened third anterior setae of *Columbicola*, and the stout second anterior setae of *Anaticola*. Some large groups of species (*Goniodes*) show variation in number, size and position of the setae so that the chaetotaxy may give specific differences.

Mouthparts.—The form of the mouthparts may be constant throughout groups of unrelated genera, or may vary considerably in related species where the differences are merely of specific value. Cummings (1916: 670) has shown, for instance, that the hypopharynx in *Ibidoeus* may be normally developed or greatly reduced.

In conclusion it can be said that the head is basically similar throughout the superfamily Ischnocera.³ Superimposed on this basically similar structure are found many variations in the superficial characters of the head—this part of the body apparently being the most closely adapted to the environment. Much of this adaptation seems to have taken place on parallel lines. This has resulted in groups of species obviously closely related by the more stable characters of the abdomen showing very different head characters, and others probably not related having similar characters of the head. This, together with the fact that in most groups of related genera there are some which have retained the primitive head characters, makes it difficult to base a supra-generic classification on the characters of the head, although it may prove that the manner by which the specialization of the head is brought about during development will indicate relationships between some of the genera. Further, the many genera which have developed modifications of the head on similar lines (as discussed under *Brüelia*) may be descendants of a common ancestor in which this was the only modification of the head possible, whereas those in which specialization has taken place on different lines (e.g., *Anaticola*, *Columbicola*, *Oxylipeurus*) are not related to the genera with the “*Brüelia*”-like heads.

³ Dr. S. Symmons (*in press*) has shown that the tentorium of the Ischnocera, unlike that of the Amblycera, is uniform in structure throughout the group; species from a number of unrelated genera were examined.

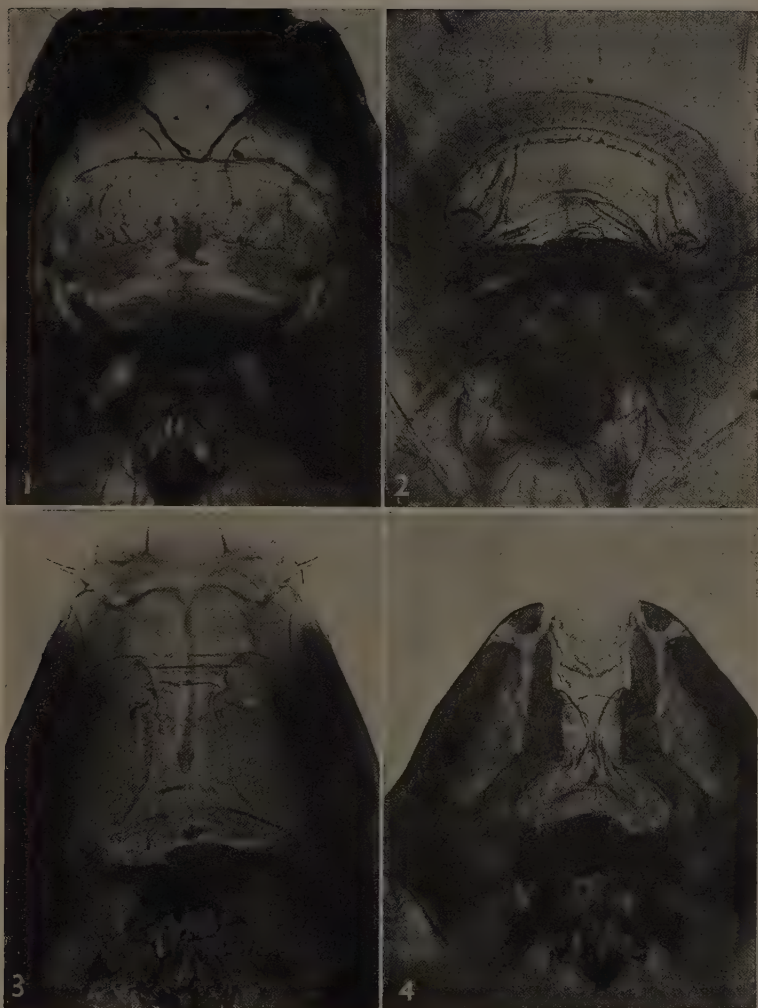
At the present time groups of species inseparable on the characters of the abdomen should probably not be separated generically on small differences in head structure, especially where they do not parasitize a related group of hosts, and hence, where the characters they have in common may be adaptive, not phylogenetic.

SUMMARY

This paper is the first of a series dealing with a reassessment of the characters used in the generic separation of the Ischnocera. The generic concept as applied to the Mallophaga is discussed. The primitive head and its specializations are described and a terminology of the structures useful in classification given. The phylogenetic significance of the variation in the characters of the head is discussed.

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Heads of Mallophaga species to show pulvinus. Fig. 1.—*Perineus* sp. Fig. 2.—*Coloceras* sp. Fig. 3.—*Anaticola* sp. Fig. 4.—*Brüelia* sp.

(Specimens mounted in polyvinyl lactophenol and photographed by H. M. Malies.)

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A NEW GENUS AND SPECIES OF MYRMECOPHILOUS
DIAPRIIDAE WITH TAXONOMIC AND BIOLOGICAL
NOTES ON RELATED FORMS.

By M. W. WING, F.R.E.S.

Manuscript received 1st July, 1950.

(Read 6th December, 1950.)

With 8 Text-figures.

Bruesopria gen. n.

Solenopsia (pars) Brues, 1936: 16.
Wing, 1949: 207.

♀. Resembles *Solenopsia* Wasmann closely. It differs notably from that genus in having: Head wider than long. Antennal shelf more shallowly excavated and with rim even. Ocelli much smaller. Eye with fewer facets. Antennal scape longer relative to head length, strongly compressed and sharply bent basally. Antennal flagellum with various differences, the most notable of which is the large, 3-segmented, capitate club. Thorax narrower than head. Pronotum visible mid-dorsally. Scutellum shallowly impressed in form of a trapezoid. Propodeum sharply constricted above anteriorly. A transverse ridge arising mid-dorsally on propodeum and extending postero-laterally to form a pair of widely separated, subacute arms, which enclose the petiolar node. Abdominal petiole relatively high and narrow, bent backwards at its mid-point, and in the form of a finger with its flat surface directed posteriorly. First abdominal segment occupying two-thirds total length of abdomen. Posterior and lateral surfaces of abdominal petiole with a thick covering of whitish hairs. No wings, or at most having vestigial, but perfectly formed wings. No high, blunt, cone-like projection antero-medially on propodeum. No dorsal groove on abdominal petiole.

♂. Unknown.

It gives me great pleasure to name this genus for Professor C. T. Brues of Harvard University in appreciation of his many kindnesses to me and as a tribute to his over fifty years of entomological work. His numerous and scholarly papers covering as they do a wide variety of topics are a most outstanding contribution to international entomology.

Genotype: *Bruesopria seeversi* sp. n.

This genus is closely allied to *Lepidopria* Kieffer, from which it differs in several particulars. Notable among these are the structure of the antennae, presence of wings and conformation of the abdominal petiole.

Excellent habitus figures of *Bruesopria* are included in the article by Professor Brues, 1936.

***Bruesopria seeversi* sp. n.** (figs. 3, 6, 8).

Wing, 1949: 207.

Structure.—♀. Length 1.3 mm. Head in lateral aspect evenly and broadly rounded above, a shallow cup-like shelf of width noticeably less than eye-width located midway

on anterior surface. In cephalic view rim of antennal cup appears even. Mouthparts located ventrally, lines from vertex to mouthparts and from shelf to mouthparts only slightly convex as seen in profile. This gives head a subglobular appearance. Eyes located well forward on head, their mid-points approximately on a level with antennal shelf. In shape the eye is nearly semicircular, its posterior margin being only slightly convex. Eye medium-sized, slightly convex, containing about 22 large facets, which are not very closely grouped. Ocelli small, forming an equilateral triangle on vertex. Mandibles small, bidentate. Other mouthparts not clearly visible on dry specimen. Antennae 11-segmented, inserted fairly closely together in shallow cup-like shelf. Scape about as long as head including shelf, strongly compressed and abruptly bent near its insertion, thicker at apex than at base. Pedicel about one-fourth the length of the scape, about as wide as long. First flagellar segment distinctly narrower than pedicel basally, but widening somewhat apically, about two-thirds as long as pedicel. The next five flagellar segments of about equal length (about half length of pedicel) and gradually becoming wider until the last one is nearly as wide as pedicel. Last three segments forming a large distinct capitate head. All three segments rounded basally, the first two truncated apically, the last rounded apically. Club about as long as scape, its first segment about as long as pedicel and somewhat wider, its next two segments becoming progressively longer, penultimate segment the widest. Antenna compact—not giving pronounced moniliform appearance as in *Solenopsia*. Thorax at its greatest width noticeably narrower than head. Pronotum visible as a narrow line mid-dorsally, but extending back to tegulae as broad lateral bands which border mesonotum. Mesonotum without notaulices (= parapsidal furrows, *sensu* Kieffer *et al.*), becoming broader posteriorly, at greatest width slightly broader than long. Scutellum separated by a fine, transverse, slightly elevated line or ridge which joins approximate mid-points of tegulae. Anterior portion of scutellum shallowly impressed in form of trapezoid, posterior portion convex, with rounded sides, and followed by a pronounced transverse furrow. Just posterior to furrow propodeal ridge arises. Propodeum sharply constricted above anterior to ridge, widening abruptly posteriorly; the propodeal ridge terminates in a pair of widely separated, subacute, postero-laterally directed arms. The posterior concavity between these arms serves as a receptacle for the abdominal petiole. Completely apterous. Legs with all trochanters long and all femora and tibiae clavate. Front tibia with a long curved spur arising medially about one-third of the way back from the apex of tibia. Abdominal petiole relatively narrow, with a high, blunt finger-like node arising from it. The node, including hairy covering, appears bent backwards at its mid-point to form an angle of about 45 degrees with respect to an imaginary line connecting bases of antennae with ovipositor. Excluding hair, petiole strongly convex anteriorly and flat posteriorly. Petiole not much narrower above than below, almost twice as high as long, about as long as wide. Second abdominal segment about two-thirds the total length of abdomen, shallowly impressed antero-laterally on each side just back of petiole, giving the effect of a low blunt ridge antero-medially. The five following segments narrow. Ovipositor with two short stout valves as seen from above.

Texture.—Body smooth and shining; head and abdomen with very high polish. Dorsum of propodeum and dorsal and lateral surfaces of petiolar scale impunctured and dull. Appendages about as shiny as thorax.

Pilosity.—Body covered with erect and suberect yellowish hairs of varied lengths. Hairs fairly numerous on thoracic dorsum, where they are short. Hairs numerous and mostly suberect on antennal funiculus, legs, and postero-dorsal half of abdomen. Eye with a few short erect hairs. Posterior and lateral surfaces of petiolar scale with tuft of long whitish hairs, which at first glance makes one take petiole to be of somewhat different shape from what it actually is.

Colour.—Medium brown. Thorax somewhat lighter than head and abdomen and with more of a yellowish tinge. Legs and antennae pale yellow. Segments of antennal club

somewhat infuscated, the last completely so, the other two only apically infuscated. Eye black. Ocelli white, but with black pigment showing below skeletal surface.

♂. Unknown.

Holotype ♀ bears the data: Wake Co., North Carolina, May 26, 1943, M. W. Wing, Berlese Sample A-43, with *Solenopsis molesta*.

This specimen is to be placed in the C. H. Seevers Collection of myrmecophiles and termitophiles. Dr. Seevers' valuable collection is now housed in the Field Museum in Chicago, Illinois.

I take great pleasure in naming this interesting species for my good friend and colleague Dr. C. H. Seevers, who is a most capable and energetic young student of myrmecophiles and termitophiles.

The single female of this species was collected near Raleigh, North Carolina (Lead Mine's Road) by means of a Berlese funnel. The sample from which it was taken consisted of surface soil together with its moss covering and came from mixed woods (predominantly deciduous). The contents of the Berlese sample bottle contained numerous specimens of *Solenopsis molesta* (Say), as an *S. molesta* nest site was selected for collecting the sample. The only forms taken other than *Bruesopria seeversi* that might have a relationship with the ants were: One specimen of a new species of *Pseudisobrachium* Kieffer (= *Isobrachium* Ashmead), and one specimen of a Pselaphid beetle. These forms will be discussed in a later paper.

***Bruesopria americana* (Brues) comb. nov.**

♀ *Solenopsis americana* Brues, 1936: 16, fig. 1.

This species is known only from a single female collected by Dr. Clyde Dennis in eastern Tennessee. The type is in the collection of Ohio State University, Columbus, Ohio. Although I have been unable to examine the type, the extended description and excellent figures in Professor Brues' article leave no doubt as to the correct generic assignment of this species.

B. americana is very closely related to *seeveri*, but differs from that species in the following particulars, as judged from the description and figures: The hind wings are preserved as vestiges. The propodeal arms are sharp and directed posteriorly. The abdominal petiole is much broader below than above. The colour is darker.

No data on pilosity were given in the description, nor indicated in the figures; therefore it is impossible to compare the two species on this basis.

The host ant is listed as *Prenolepis parvula* Mayr. It seems probable that this represents only a part of the story. If so, it is quite misleading. I shall indicate what I consider to be the true host relationship in my general discussion below.

As has been implied in the discussion of both species of *Bruesopria*, there are no actual observational data which make it possible to state with certainty that these species are true guests of ants. And in the case of *americana* there is even some question as to the true host species.

However, since this genus is very closely related to *Solenopsis* and *Lepidopria*, both of which are true guests, or symphiles, of *Solenopsis fugax*, it would seem probable that the species of *Bruesopria* are symphiles associated with the North American counterpart of the European *fugax*, viz., *Solenopsis molesta*. My explanation of the host record of *Prenolepis parvula* (now *Para-*

trechina (*Nylanderia*) *parvula* (Mayr)) in Professor Brues' paper (1936) is as follows: In the North Carolina and Tennessee area *Solenopsis molesta* is a very common species. It is called a lesteobiotic or thief ant because of its habit of founding its colonies adjacent to the nests of larger ant species. The *S. molesta* workers then pilfer food from the nests of the larger species, but the larger ants cannot get into the *molesta* nest because of the extremely small interconnecting galleries. From about eight years of study of this species in Wake Co., North Carolina, I would estimate that a little over half of the colonies of *molesta* are in association with the nests of larger species, while the rest of their colonies are independent of other nests. A collector seeking any of the larger species might easily overlook entirely an associated *molesta* colony. I believe that Dr. Dennis in collecting the specimen of *Bruesopria americana* from the *Paratrechina parvula* colony overlooked an associated *Solenopsis molesta* colony. I wrote Dr. Dennis about this matter, and he agreed that this was quite possible. He was unable to check on the matter, however, as his collection was then located in a distant town.

It is to be hoped that further specimens of this genus will be collected and studied in artificial nests by more than one biologist. It is only by such study that we can learn the facts.

The problem of distribution in this apterous or near-apterous genus is interesting. If one of these minute wasps were to walk out of a colony in search of a new colony it could under certain circumstances be picked up and passively moved over considerable distances by air currents (cf. Glick, 1939).

Another possibility is associated with an alternative method of colony founding that is not infrequently utilized by *Solenopsis molesta*. This method may be considered hesmosis, even though only one or two workers accompany the young founding queen. In this species the queen is considerably larger than the worker, making it possible for her to carry one or two workers attached to her legs when flying out to found a new colony. Brown (1945) reports that some 20 per cent. of the queens of *molesta* in the Philadelphia area carried one worker or rarely two workers on their legs. Whether or not a *Bruesopria* female could or would make use of such a convenient method of transportation to new territory is an open question.

Hölldobler (1936) states that he has never observed this hesmotic behaviour in the European *fugax*. Even if it does occur in *fugax*, the *Solenopsis* females are a little too large to ride on a leg of a queen of the host species.

Solenopsis Wasmann.

Solenopsis Wasmann, 1899: 127.

♀ See diagnosis under *Bruesopria* above.

♂. Unknown.

Species in two different genera of DIAPRIIDAE have been described as males of *Solenopsis*. For a discussion of these forms see under *Geodiapria longiceps* Kieffer and *Lepidopria pedestris* Kieffer.

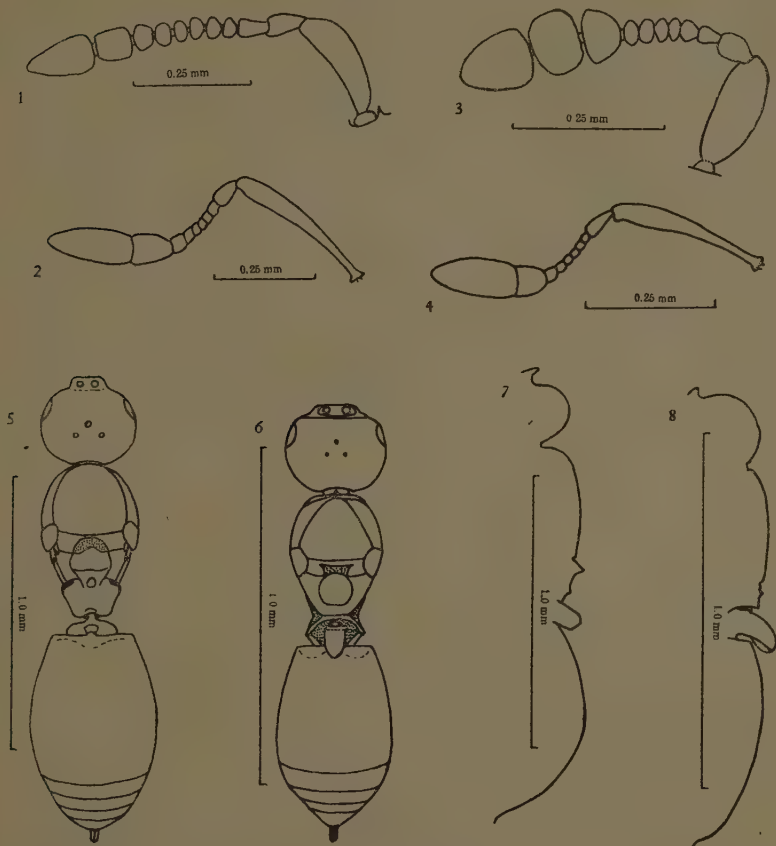
Inasmuch as no males have ever been taken, but numerous females of the single species of this genus have been taken (Gösswald, 1929, had taken over 150 ♀), it seems quite likely that we are dealing here with a thelytokous species, as is the case in *Nemeritis canescens* (Grav.) (ICHNEUMONIDAE).

Genotype: *S. imitatrix* Wasmann, 1899. This genus is known only from Continental Europe, no British specimens having been taken to date.

Solenopsia imitatrix Wasmann (figs. 1, 5, 7).

♀. Wasmann, 1891 : 25.

♀. Janet, 1897 : 51.

♀. *Solenopsia imitatrix* Wasmann, 1899 : 127 ; Long, 1902 : 13, fig. 7a ; Ashmead, 1902 : 15 ; Wasmann, 1909 : 66, 171, pl. 3 ; Kieffer, 1911 : 873, pl. 22 ; 1911a : 17, pl. 2, fig. 3 ; Wasmann, 1915 : 26, 256, 346, 392 ; Kieffer, 1916 : 20, figs. 7, 7a ; Wasmann, 1925 : 91 ; Ferrière, 1927 : 282 ; Hölldobler, 1928 : 139 ; Gösswald, 1929 : 111.

FIGS. 1-8.—(1)-(4) Antenna of (1) *Solenopsia imitatrix* Wasm., ♀ ; (2) *Solenopsis fugax* (Latr.), ♀ ; (3) *Bruesopria seeversi* Wing, ♀ ; (4) *Solenopsis molesta* (Say), ♀ ; (5), (6) Dorsal view of (5) *Solenopsia imitatrix* Wasm., ♀ ; (6) *Bruesopria seeversi* Wing, ♀ ; (7), (8) Lateral profile of dorsum of (7) *Solenopsia imitatrix* Wasm., ♀ ; (8) *Bruesopria seeversi* Wing, ♀.

Since Father Wasmann in preparing the description and figures for this species failed to include certain points of interest to the present-day student, I asked my good friend Father Jos. van Boven if he could send me an authentic

specimen of *S. imitatrix* for study. He very kindly obliged by sending me two specimens, one of which was the type. A redescription of *S. imitatrix* Wasmann based on the type-specimen follows.

Structure.—♀. Length 1.7 mm. Head in lateral aspect evenly rounded above; a moderately deep cup-like shelf, noticeably wider than eye, located midway on anterior surface. In cephalic view rim of antennal cup uneven with a more or less blunt point projecting upward between antennal scapes. Mouthparts located ventrally; profile line from vertex to mouthparts and from shelf to mouthparts convex. This gives head a globular appearance. Mandibles of medium size, clearly bidentate. Other mouthparts not clearly visible on dry specimen. Eyes located well forward on head, their mid-points approximately on a level with antennal shelf. Eye elliptical, posteriorly truncated parallel to major axis so as to cut off about 15 per cent. of minor axis. Complete minor and major in ratio of 3:4. Eye of moderate size, slightly convex, containing 32 medium-sized axes facets, which are fairly closely spaced. Ocelli large, forming equilateral triangle on vertex. Antennae 11-segmented, inserted fairly closely together in moderately deep cup-like shelf. Scape thick, tubular, nearly straight, and about two-thirds as long as head including antennal shelf. Pedicel nearly one-third length of scape, somewhat longer than wide. First flagellar segment about as wide and nearly as long as pedicel. Following six flagellar segments all of about same width as, and all noticeably shorter than first flagellar segment. Last two segments forming a definite club. Club somewhat shorter than scape. First segment of club about as long as pedicel and noticeably wider. Antenna with loose moniliform appearance. Thorax at its greatest width noticeably wider than head. Pronotum not visible mid-dorsally, but seen laterally as narrow bands bordering the mesonotum and extending back to tegulae. Mesonotum without notaulices (= parapsidal furrows, *sensu* Kieffer *et al.*), becoming broader posteriorly, at greatest width noticeably broader than long. Scutellum separated by a fine transverse, slightly elevated line or ridge extending between the tegulae. Anterior portion deeply impressed in something of the form of an inverted crescent. This concavity followed posteriorly by a low convex surface. A high, blunt, cone-like projection is located antero-medially on propodeum. Propodeum broad anteriorly as seen from above; at each outer angle there is a black upraised ridge giving the appearance of a fine, postero-laterally directed tooth. Wasmann's illustration of these structures is exaggerated and misleading. Propodeum gradually narrowing posteriorly. Short wing stubs clearly showing. It would appear that this specimen was once fully winged, and that later wings had been broken off, or perhaps bitten off by the ants. Legs with all trochanters fairly long and all femora and tibiae clavate. Front tibia with a long, stout, curved spur arising medially about one-fifth of way back from apex of tibia. Abdominal petiole broad, subrectangular in profile, its anterior surface irregularly convex, and posteriorly with a broad groove dorso-medially. Below the line which terminates the groove, petiole is broadly recessed throughout. Second abdominal segment about five-sevenths the total length of abdomen, the following four visible segments narrow. Ovipositor with two short stout valves.

Texture.—Body smooth and polished, appearing quite shiny, except for propodeal spine, antero-medial part of petiolar scale, and dorso-lateral parts of antennal cup, which are impunctured and appear somewhat dull. Appendages are not as shiny as body.

Pilosity.—Body and appendages covered with fairly numerous yellowish hairs of varied lengths. Hairs erect and suberect. Hairs relatively more numerous dorsally than ventrally. Propodeum and appendage with relatively thick coverings of hair. Eye with a few erect hairs of varied lengths.

Colour.—Dark brown. Second abdominal segment as seen from above somewhat lighter and with more of a yellowish tinge than rest of body. Legs and antennal scape brownish yellow. Antennal funiculus of uniform darker brownish yellow than scape. Propodeal tooth and recurved spines, edges of tegula, mesonotum and scutellum, and postero-dorsal and lateral part of abdomen infuscated. Eye black. Ocelli white with

black pigment circles showing toward centre of the imaginary triangle which they form.
♂. Unknown.

Type ♀:—Bears the following data: 3/5.98, Exau, C. *Solenopsis*, *Solenopsis* C. *pratensis*, p. 4. Location of type: Wasmann Collection.

Other ♀:—Length, 1.6 mm. Bears the data: C. *Solen. fugax*, Würzburg, 4/27, Hölldobler.

The records from the literature are: FRANCE (Beauvais), HOLLAND (Exaeten, the type locality), ITALY (Oriolo) and GERMANY (Würzburg).

This species is always found in association with *Solenopsis fugax*, either in simple colonies or in compound colonies with other ant species. The type female was taken from a *Solenopsis fugax-Formica pratensis* colony.

Father Wasmann gives the length of the type female as 1.75 mm. Kieffer (1916) lists 1.75 to 2 mm. as the range of length for this species. Judging from the specimen collected by Dr. Hölldobler in Würzburg, the lower figure in this range should be 1.6 mm.

Solenopsis imitatrix was first found by Father Wasmann with *Solenopsis fugax* (Latr.) (with *Formica rufibarbis* Fabr.) in the spring of 1884 at Exaeten (Holland). The single specimen was sent to Professor A. Förster, who stated that it was a new genus closely related to *Diapria*. Förster died shortly thereafter, and the specimen found its way into another collection. Because of this unfortunate occurrence Wasmann was able to describe this form (1899) only after finding another specimen in May of 1898 in a colony of *Solenopsis fugax* (with *Formica pratensis* Retz.).

Wasmann (1891) reported on the behaviour of this specimen as it occurred in an artificial nest of *Solenopsis fugax* while it was still unnamed. He felt at the time that it should be assigned to the indifferently tolerated guests, as the ants paid no attention to it, and at no time did he observe feeding of the guest by the ants.

Janet (1897), without proposing a name for this form, stated that he had found it on several occasions in the nests of *Solenopsis fugax* at Beauvais. Janet studied this form in vertical artificial nests. Inasmuch as the guest is nearly black whereas the associated ants are yellow, it was very easy to follow the movements of the guest. He found that, although the ants paid little attention to it in the galleries, the guest was differently treated in the small chambers of the nest. Here a few weeks after setting up the nest he often observed that the ants licked the guest as if to clean it. Also the guest was observed to tap obstinately with its antennae the head of the ant occupied with it. Finally on two or three occasions the guest was observed to place itself mouth to mouth exactly in front of a worker. Janet at this point stated his intention of observing such behaviour more carefully to determine if liquid nourishment was actually passed between them.

Wasmann (1909, 1915, 1925) views *Solenopsis imitatrix* as a true guest. He does not make it clear whether his view is based only on Janet (1897), or also on additional observations on his part. Furthermore, he states that the young stages develop as parasites of the ant brood. At no place are data presented to substantiate this, and thus I presume that it is a guess on his part. Such a guess might well have been based on the observations that he had made on *Tetramopria*.

Hölldobler (1928) presents an excellent account of his observations on this species. In March, 1922, he began observing a female in a nest with

Solenopsis fugax. The guest was given very little attention until along in May. At this time he saw one or more ants licking her body, and observed that she was fed by the ants. Feeding was preceded by an antennal tapping of the ants' antennae, although this ant species normally uses only a light tap of antennae in soliciting food from a sister. It was noted that *S. imitatrix* stayed by preference with the ant brood. In licking her the ants seemed to prefer the neck, antennae and petiole. She not infrequently stroked the licking ants with her antennae. The ants often dragged her about in the nest. In mid-June the wasp disappeared from the nest without leaving a trace.

From the Hölldobler account it would appear that Father Wasmann did not bear with his original colony long enough to see any more than indifference on the part of the ants toward their guest.

It is interesting to note the *S. imitatrix* utilized a method of food solicitation that differs significantly from that normally used by two host ants. It was apparently close enough to the normal method of *Solenopsis fugax*, however, so that the food was received.

The fact that by preference *S. imitatrix* stayed with the brood is good circumstantial evidence that the younger stages of this guest develop as parasites of one of the immature stages of the host ant. This view is strengthened by the fact that the family DIAPRIIDAE is composed of species that are parasitic on various other insects.

Inasmuch as the population level of *S. imitatrix* is presumably never very high per ant colony, such a parasitic species could presumably be borne by all except the weakest colonies without any significant harm.

Dispersal in space presents no problem as *Solenopsis* ecloses as a fully winged wasp and could therefore actively fly some distance to new colonies. In fact the studies by Glick (1939) would indicate that a species of this size might be passively carried by air currents to very great distances. Such a flight would have to be made shortly after eclosion, as older wasps are almost always without wings. It is believed that the ants chew their wings off at the base (cf. Gösswald, 1929).

One is curious as to why the ants are duped into graciously accepting such a creature into their midst. Typically a strange insect of this same general size, if dropped into a formicary would be chased out post-haste, or be torn up on the spot. It follows then that the *Solenopsis* female has something, even if it does take the ants a while to appreciate it. In such cases as this it would seem to me that we can determine the true story only by a careful study of adequate living material. Quite probably in some cases, at least, an experimental approach would be indicated. And above all each new species and new relationship must be studied as a new problem on its own merits, for we have no assurance that only one method is operative. Nevertheless let us see if we can determine on a speculative basis what factors might be of importance. This seems to me to be a perfectly justified approach if it is properly labelled as speculation, and there is no better immediate approach to the problem.

The inherited mechanisms with which an ant worker is endowed, presumably at eclosion, are capable of coping with the problems of obtaining food, tending the brood, etc. Such duties involve the perception of odours, textures, etc. The evidence would indicate that these devices which tend to bind the colony

are necessary for continued colonial life, but are extremely fixed and rigid. Thus any small organism which becomes sufficiently adapted structurally and behaviouristically to gain favour from the ants may exploit their colonies with impunity. An excellent series of all stages in the development of myrmecophily is to be seen in the Coleoptera, where *Quedius* and *Atemeles* mark the generalized and specialized end-points respectively.

If we examine the observable likenesses and differences between *Solenopsis imitatrix* and *Solenopsis fugax* (cf. figs. 1, 2), we find that visually they are not too dissimilar. However, the very poor visual ability of this ant species, coupled with its hypogaic existence, would seem to relegate vision to a place of little or no importance.

As for integumentary texture and pilosity, however, there is a good possibility that it may be of importance. Both ant and guest are smooth, and both have much the same pilosity. The pilosity of the antennae is very close between these two species. Elsewhere on the body the ant has somewhat longer, coarser and less numerous hairs than the guest. As the ants are specialists in the perception of textures, such a close relationship between ant and guest on this basis may well be of importance.

Finally the matter of odours and possibly taste come under consideration. Every student of the Hymenoptera is aware that ants and parasitic forms are ultraspecialists in the matter of olfaction. Although the sites of production of olfactory substances are not apparent through ordinary microscopic examination, we are aware on other bases that certain odours do play an important part in the colonial life of the ants. The question naturally arises as to whether *Solenopsis* possesses only the nest odour of the ants by virtue of having enclosed in the nest and mingled with the ants, or whether she possesses certain special odours of her own that are attractive to the ants. Probably both kinds of odours play a part in this symphiliic relationship. It is interesting to recall in this connection that Hölldobler observed that by preference the ants licked certain parts of her body. One of these regions was the neck. The neck hairs in *Solenopsis* and related genera are yellowish to white. The colour possibly varies with the age of the specimen before and/or after death. In *Tetramopria* these hairs are golden yellow, reminding one of the Trichomes of some of the myrmecophilous Coleoptera. Wasmann made quite a point of this characteristic of *Tetramopria*. He states that the development of these golden hairs is certain evidence that *Tetramopria* is a true symphile. His observations indicated that the host ants, *Tetramorium caespitum*, spent much time in licking these golden neck hairs, much in the same way as they did in the case of the Pselaphid, *Chennium bituberculatum* (Latr.). The difficulty with Father Wasmann's stand seems to be that he considered that only golden neck hairs could subserve the function of bringing about a true myrmecoxenic relationship. I am sure that few modern students will wish to make such a simplifying assumption in the face of the complexity and diversity of possible mechanisms which may lead to the attainment of symphily. In justice to Father Wasmann, to whom all students of myrmecophiles owe a very great debt of gratitude, however, it should be pointed out that had he known more of the ethology of *Solenopsis* his stand on this matter would probably have been modified.

A possible experimental basis on which to determine the relative importance of such matters as textures, pilosity and odours occurs to me. If one were to

make up colonies of a suitable species of ants by stocking a newly made observation nest with pupae that were about to eclose, it would be possible to introduce the pupae of any species of insect without instigating an immediate war. The subsequent developments in such an artificially compounded colony could be observed for a number of different species of "guests." By working with a number of species of various sizes, textures, degrees of pilosity, etc., one could collect much interesting data, some of which, at least, would probably be of use in interpreting naturally occurring myrmecophilic relationships. It would seem desirable to try species that were not normally myrmecophiles, as well as known myrmecophiles of varied degrees of development toward symbioly.

Auxopaedeutes Brues.

Auxopaedeutes Brues, 1903 : 126.

♀. Inasmuch as this genus might be confused with *Bruesopria*, it seems worth while to indicate the more outstanding differences between them. *Auxopaedeutes* has a 12-segmented antenna with a 2-segmented club. Its upraised, ant-like petiole is lower, lying under rather than between the propodeal teeth. The shelf for the insertion of the antennae is shallow, and covers a much larger area on the front of the head than is the case in *Bruesopria*.

♂. Unknown. This genus is known only from North America.

Genotype : *A. sodalis* Brues.

Auxopaedeutes sodalis Brues.

♀. *Auxopaedeutes sodalis* Brues, 1903 : 127, pl. 1 ; Kieffer, 1916 : 31, figs. 10, 10a (= 1).

A single specimen of this species was collected by Prof. W. M. Wheeler in a nest of *Solenopsis molesta*. The exact locality was Bull Creek, Travis Co., Texas. No biological data on the ant-guest relationship are available. In using Kieffer (1916) one must guard against the figures of this species, as they are quite unreliable.

Auxopaedeutes lyriformis Brues.

♀. *Auxopaedeutes lyriformis* Brues, 1910 : 82 ; Kieffer, 1916 : 32.

This species was taken as a single specimen from a nest of *Solenopsis molesta* by Prof. W. M. Wheeler. The locality was Forest Hills, Boston, Massachusetts. No biological data on the ant-guest relationship are available.

In addition to these two species, each of which is based on a single specimen, there are two other specimens in collections.

On 14th July, 1946, I collected a single specimen from a compound nest of *Solenopsis molesta* and *Paratrechina* (*Nylanderia*) *parvula* (Mayr.). The locality was Siler City, Chatham Co., North Carolina. Inasmuch as the collection was made with an aspirator (= exhaustor), I did not realize that I had taken this tiny wasp until the colony sample was examined microscopically in the laboratory. Examination of this specimen indicated that it was either *sodalis* or a closely related species. As to the host relationship, it is my considered opinion that *Solenopsis molesta* and not *P. parvula* was the host species. I believe that further investigation will show that the species of this genus are true myrmecophiles. My reasons for such a view are the same as in the case of *Bruesopria*.

The fourth specimen of *Auxopaedeutes* is in the Brues collection. Professor Brues told me about its existence in conversation. He felt that it might possibly be *sodalis*, but was not sure since he had not studied it carefully. I have no locality or biological data on this specimen.

I hope in the not distant future to be able to make a trip to the Museum of Comparative Zoology in Cambridge, Massachusetts. If this becomes possible I shall carefully study their three specimens and write a synopsis of this interesting genus.

Lepidopria Kieffer.

Lepidopria Kieffer, 1911 : 869.

L. Kieffer, 1916 : 22.

Lepidopria pedestris Kieffer.

♂. *Solenopsia* sp., Wasmann, 1909 : 172.

♀. *Lepidopria pedestris* Kieffer, 1911 : 870.

♂. *Solenopsia castanea* Kieffer, 1911 : 872.

♂. *S. castanea* Kieffer, 1911a : 17, pl. 1, fig. 16 ; pl. 2, fig. 12.

♀. *Lepidopria pedestris* Kieffer, 1916 : 22.

♀♂. *L. pedestris* Ferrière, 1927 : 282, figs. 1, 2.

♀♂. *L. pedestris* Hölldobler, 1928 : 140.

♂. *L. pedestris* Gösswald, 1929 : 111.

This European species is a true myrmecophile. Both sexes eclose with fully developed wings, but in most older specimens of both sexes only the wing stumps are left. This déalation is sometimes unilateral, sometimes bilateral. It would seem quite likely that the host ants remove the wings of their guests. The excellent studies of Hölldobler indicate that the *Lepidopria* male is treated in a friendly way, getting much the same treatment as *Solenopsia*. In the case of feeding, however, the *Lepidopria* male reacted differently from *Solenopsia*. Upon meeting a worker ant the male would tap on it slowly with its club-like fourth antennal segment and stroke its cheeks with the forelegs. When the male had left this ant, the next one that was met was handled in the same way.

The host ant is *Solenopsis fugax* (Latr.). The statement by Wasmann (1909) that the host of *Solenopsia castanea* was *Solenopsis geminata* (Fabr.) is clearly an error, since Kieffer listed *S. fugax* as the host.

Lepidopria aberrans Brues.

♀. *Lepidopria aberrans* Brues, 1916 : 126, fig. 1.

This North American species in all probability represents a new genus that is closely allied to *Lepidopria* and *Bruesopria*. Until I am able to examine the type it would seem unwise to alter its present generic allocation.

There is no evidence that would indicate that this species is a myrmecophile, despite its ant-like appearance.

Loxotropa A. Förster.

Loxotropa Förster, 1856 : 122.

L. Kieffer, 1916 : 167.

Loxotropa californica Ashmead.

♀. *Loxotropa californica* Ashmead, 1893 : 415; Wasmann, 1909 : 68; 1915 : 346; Kieffer, 1916 : 190.

Father Wasmann (1915) presents an interesting account of what he believed to be this species. I hope by later collecting in the Wisconsin area to find out exactly the species to which he was referring.

The first record of *L. californica* (det. Ashmead) is from Westcliff, Colorado. The host ant was listed as *Solenopsis debilis* (syn. of *S. molesta validiuscula* Em.). The second record is from Prairie du Chien, Wisconsin. In this case Wasmann made the determination himself. The host ant was listed as *Solenopsis debilis* (syn. of *S. molesta* (Say)). The host ant in this case was in a compound nest with *Formica exsectoides* Forel. This black wasp was stated to be common in *Solenopsis* colonies in the Wisconsin area. The Wisconsin specimen appeared to have had its wings bitten off at the roots by the host ants.

Loxotropa nigricornis var. *subterranea* Kieffer.

♂. *Loxotropa nigricornis* var. *subterranea* Kieffer, 1911 : 938.

♂. *L. nigricornis* var. *subterranea* Kieffer, 1916 : 182.

♂. *L. subterranea* Donisthorpe, 1927 : 106.

It is not clear whether this British species is a myrmecophile or not. *L. subterranea* has been reported from a *Solenopsis fugax-Lasius flavus* (Fabr.) colony and also from a colony of *Lasius niger* (L.). It is quite possible that the occurrence of this species here is correlated with some habit other than true myrmecophily.

Tetramopria Wasmann.

♂♀. *Tetramopria* Wasmann, 1899 : 127; 1909 : 69; Kieffer, 1911 : 887; 1916 : 67.

There are five described forms : *T. aurocincta* Wasmann, 1899; *T. aurocincta* var. *rufescens* Kieffer, 1911; *T. cincticollis* Wasmann, 1899; *T. donisthorpei* Kieffer, 1911; and *T. donisthorpei* var. *femoralis* Kieffer, 1911.

The studies of Wasmann (1909) and Donisthorpe (1927) indicate that the species of this genus are highly developed myrmecophiles. The host ant is *Tetramorium caespitum* (L.). Notes on some aspects of the relationship of the species of this genus to their host ant are discussed under *Solenopsis imitatrix* Wasm.

Trichopria Ashmead.

Trichopria Ashmead, 1893 : 407, 431.

Trichopria (*Trichopria*) *inquilina* (Kieffer).

♀. *Diapria inquilina* Kieffer, 1904 : 56.

♀. *Trichopria inquilina* Kieffer, 1911 : 997.

♀. *T. (Trichopria) inquilina* Kieffer, 1916 : 86.

♀. *T. inquilina* Hölldobler, 1928 : 140.

♀. *T. inquilina* Gösswald, 1929 : 111.

This European species may be a true myrmecophile, but the case is not too clear. Hölldobler has studied a female in an artificial colony. It was found that this species was rather timid and seemed to prefer to be away from the ants. When a meeting did occur and the ant touched the wasp's wings with its antennae, the ant's mandibles were spread open, as in fright, and the wasp was chased for a distance. It is possible that it was only the wings which caused this reaction. If so, it is possible that at a later date the wings would be removed as in *Lepidopria*, etc., leading to more friendly relations between host and guest. On the other hand, it is possible that *T. inquilina* is not a true guest, or, at least, not a highly developed guest. Dr. Hölldobler was unable to decide this point as the colony dried out and all of its members died.

While the colony was still in good shape Hölldobler observed love play between a *Trichopria inquilina* ♀ and a *Lepidopria pedestris* ♂. The male was on the back of the female for at least 15 hours! The antennal caressing of the female by the male, so common among parasitic Hymenoptera, was observed. Despite the long period of preliminary play no copulation was attempted so far as Dr. Hölldobler could determine.

The interesting feature of this interspecific union is the length of time that was consumed. On the basis of my studies (unpublished) of sexual behaviour in various groups of parasitic Hymenoptera, such love play lasts normally for only a short time—a matter of seconds or minutes. In cases of intraspecific, male, homosexual play the normal time is shortened, presumably because of the lack of a normal sequence of suitable stimuli.

The host ant of *T. inquilina* is *Solenopsis fugax* (Latr.).

Myrmecopria Ashmead.

Myrmecopria Ashmead, 1893 : 407, 446.

Myrmecopria mellea (Ashmead).

♂. *Loxotropa mellea* Ashmead, 1887 : 196.

♀. *Myrmecopria mellea* Ashmead, 1893 : 447, pl. 18, fig. 8.

♀. *M. mellea* Kieffer, 1916 : 252, fig. 60.

Recent collecting by Mr. E. O. Wilson, Jr., in Alabama has turned up what is apparently this long-lost genus. Mr. Wilson took female specimens with two different species of *Eciton* (Subgenus *Neivamyrmex*). Thus Ashmead's comment, "By far the most remarkable Diapriid yet discovered, and exhibiting a most remarkable resemblance to certain ants," takes on new meaning. Ashmead described *mellea* on what he believed to be the male. Later he apparently decided that this specimen was a female. It would appear that he then made the switch in sexes without explanation. This matter needs investigation.

Myrmecopria mellea is but one of many ecitophilous species. Father Borgmeier (1939) has listed 25 species mostly from Brazil. Many of these forms are highly modified so as to resemble their host ant. The abdominal petiole is ant-like in a number of the ecitophilous forms.

Geodiapria Kieffer.*Geodiapria* Kieffer, 1911 : 896.*Geodiapria longiceps* Kieffer.♀. *Solenopsis imitatrix* (♂) Wasmann, 1899 : 127.♀. *Loxotropa longiceps* Wasmann, 1909 : 172 ; syn. nov.♀. *Geodiapria longiceps* Kieffer, 1911 : 897.♀. *Loxotropa longiceps* Wasmann, 1915 : 256, 347 ; syn. nov.♀. *Geodiapria longiceps* Kieffer, 1916 : 146.

This European species was taken from a *Solenopsis fugax*-*Formica sanguinea* Latr. colony in Holland, and originally described as the male of *Solenopsis imitatrix* by Wasmann. To my knowledge there is no evidence to show that it is a true myrmecophile.

Ashmeadopria Kieffer.*Ashmeadopria* Kieffer, 1911a : 59.*Ashmeadopria formicina* (Kieffer).♀. *Diapria* (*Tropidopria*) *formicina* Kieffer, 1911 : 953.♀. *Ashmeadopria formicina* Kieffer, 1916 : 124.

This species has been listed as a guest of *Solenopsis fugax* in Luxembourg. Only further data will clarify its status.

Adeliopria Ashmead.*Adeliopria* Ashmead, 1902 : 15.*Adeliopria longii* Ashmead.♂♀. *Adeliopria longii* Ashmead, 1902 : 15.♀. *A. longii* Long, 1902 : 13, fig. 7.

This American species was reared from puparia of *Ceratopogon wheeleri* Long, which were taken from what appeared to be an abandoned ant nest. Statements by Ashmead and Long that this genus is closely related to *Solenopsis* are misleading. My examination of the type did not indicate a very close relationship between this genus and *Solenopsis*. This species is surely not a myrmecophile.

Two other genera which deserve attention are *Cyathopria* Kieffer and *Trimicrops* Kieffer. *Cyathopria rufiventris* Kieffer has an upraised petiolar scale which is ant-like in appearance. Ferrière (1927) suggests that this species will probably be found to be a myrmecophile. Brues (1936) points out the fact that *Trimicrops* is probably quite closely related to *Bruesopria* and *Auxopaedeutes*. Although Kieffer places *Trimicrops* in the CALLICERATIDAE, it is in all probability a Diapriid.

SUMMARY.

This paper contains a new genus, a new species, and a new combination. An extended redescription of *Solenopsis imitatrix* Wasmann is given, together with brief taxonomic notes on some related species. Certain aspects of the biologies of the species included are discussed. Chief emphasis is placed on the evidence for, and the degree of myrmecophily. Particular attention is given to those forms which are associated with *Solenopsis fugax* (Latr.) and *S. molesta* (Say). This paper is to be considered not as an exhaustive treatise,

but rather as an initial contribution to the study of this fascinating Alice-in-Wonderland society.

The illustrations were made by the use of an ocular cross-hatched disc. Each drawing has its own reference scale beside it. The descriptions were drawn up under 120 magnifications. The light source was a combination of sunlight and artificial light.

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including morphology of the abdomen, host-
parasite relationship and geographical distri-
bution, and with descriptions of five new
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2
A RECORD OF THE STREBLIDAE FROM THE PHILIPPINES AND
OTHER PACIFIC ISLANDS, INCLUDING MORPHOLOGY OF THE
ABDOMEN, HOST-PARASITE RELATIONSHIP AND GEO-
GRAPHICAL DISTRIBUTION, AND WITH DESCRIPTIONS OF
FIVE NEW SPECIES (DIPTERA).

By B. JOBLING, F.R.E.S.

(Wellcome Laboratories of Tropical Medicine.)

Manuscript received 25th October, 1950.

(Read 6th December, 1950.)

With 2 Maps and 10 Text-figures.

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INTRODUCTION.

THE present record of the STREBLIDAE from the Philippines and other Pacific Islands is based upon the examination of 361 specimens collected by members of the Chicago Natural History Museum in 1946-1947, and a few specimens collected by the Crane Pacific Expedition. In this record I have also included 40 specimens collected by Major Robert Traub, in Burma. A few specimens of the genus *Ascodipteron* from the Philippines are not mentioned here because their correct identification is impossible without an examination of the types of previously described species from Indonesia.

With the exception of the names of the collectors specially mentioned, the rest of the specimens from the Philippines was collected by Mr. H. Hoogstraal. The material was kindly submitted to me by Mr. R. L. Wenzel, of the above-mentioned institution, and for his information concerning the specimens and their hosts, and most of all for his permission to retain a few duplicates and the paratypes, I wish here to express my thanks. I am also very grateful to Mr. R. W. Hayman, of the British Museum (Natural History), for checking my list of the bats, and to Mr. H. Oldroyd of the same Institution for obtaining for me the type of *Raymondia pagodarum* Speiser, from the Vienna Museum.

The presence of many specimens of the same species in the collection gave me an opportunity to investigate some obscure points of the external anatomy of the thorax and especially of the abdomen, which I was unable to do before owing to shortage of material. The result of this investigation is incorporated in the present paper, which has also a new key to the species of the genera *Raymondia* and *Nycteribosca*.

ON SOME CHANGES IN THE TERMINOLOGY OF THE PARTS OF THE THORAX.

In my former papers on the STREBLIDAE, the parts of the thorax which lie ventrally to the scutellum and dorsally to the hypopleura were called the metapleura, whereas in fact each of them is composed of two parts—the pleurotergite, and the modified thoracic squama or the lower calypter (fig. 6 c). As in Calypterae, the anterior part of each thoracic squama lies close to the posterior ridge of the scutellum, but its posterior part, owing to the postero-ventral shifting of the sclerites of the thorax, is separated from the ridge. The squamae of the genus *Nycteribosca* are of two different forms. In some species they are broadly rounded (fig. 4 A), whereas in the other their posterior part is papilliform or conical (fig. 6 A, B and C). Although not sclerotized as are other parts of the thorax, they are quite distinct in spirit-preserved specimens and in those which are mounted in Canada balsam. They have clear-cut characters in this genus and are very convenient for the subdivision of the species in the key. In *Raymondia* they are reduced and are not so conspicuous as in the above-mentioned genus. In both subfamilies of the American STREBLIDAE they form together with the pleurotergites very conspicuous rounded or more or less conical projections in the posterolateral parts of the thorax.

The presence of the thoracic squamae shows that the other lobe of the basal part of each wing, which lies between the alula and the squama, is the wing squama or the upper calypter (fig. 9 A, ca). The upper calypters are present in all the STREBLIDAE which have functional wings. They are usually strongly sclerotized and bear a few long setae.

The STREBLIDAE were regarded by me (Jobling, 1936a) as specialized Acalypterae, but the structure and the position of the thoracic squamae support the view of Hennig (1941), who refers them to the Calypterae. This view is also supported by the presence in the STREBLIDAE of the posterior calli (fig. 6 A, c), which, like those of other Calypterae, are situated at the lateral parts of the scutum, and are formed by the depression extending from the base of the wings to the antero-lateral parts of the scutellum.

THE MORPHOLOGY OF THE ABDOMEN.

The external structure of the abdomen of these Diptera was briefly described by Speiser (1900), and in the male of *Paradyschiria fusca* (syn. of *P. dubia* Rudow) by Cole (1927). In several species of different genera it was figured in my descriptions of these flies, and that of the male of *Nycteribosca kollari* Frauenfeld (syn. of *N. africana* Walker), by Hennig. But owing to the great modification of the abdomen in these flies and to shortage of material, no real attempt has been made to homologize its different parts with those of the abdomen of the Cyclorrhapha. The following description is

based upon the study of this region of the body in all the subfamilies of the STREBLIDAE.

The Female Abdomen.

The female abdomen is almost entirely membranous, and has only a few sclerites in the basal and the distal parts. It ends in the proctiger of Crampton (1942) or "anal segment" of other investigators. As in *Cyclorrhapha* the tergites of the first two abdominal segments are united forming a syntergite (fig. 2 A, 1 + 2t). In some species of the genus *Nycteribosca* the second tergite (2t) is separated from the first (1t) by a very thin but distinct suture, along which the cuticle is depressed (fig. 8). The lateral parts of the first tergite are usually elevated and have each a patch of small setae, while those of the second tergite form large lobes, which bear very long setae. These tergites have two well-developed internal ridges (shown by dotted lines in fig. 8), which articulate the abdomen with the processes of the metathorax and also serve for the attachment of the abdominal muscles. According to Young (1921), who described these ridges as "adventitious sutures," they are better developed in the Calypterae than in the Acalypterae. The higher development of these ridges in the STREBLIDAE is another proof that these flies belong to the Calypterae.

The sternite of the 1st segment (1s) is a very small curved plate, whereas that of the 2nd segment (2s) is large and usually bears a large triangular patch of small setae in the middle (fig. 2 A).

Between the 2nd segment and the small sclerites near the proctiger and the genital opening the abdomen of the NYCTERIBOSCINAE is entirely membranous. As regards the homology of these small sclerites, it can be established by their position in relation to the following parts: the genital opening or gonopore, which is located between the 8th and the 9th sternites; the proctiger (*pr*), which, according to Crampton, is formed by the union of the 10th and the 11th segments; and by the position of the abdominal spiracles.

The abdominal spiracles, as those of the Calypterae, are situated in the tergites, or in the tergal parts of the abdomen when the tergites are absent (fig. 2 A), and their number is not the same in the different subfamilies of these Diptera. Thus, there are six pairs of spiracles in the NYCTERIBOSCINAE, seven pairs in the TRICHOHINAE and the STREBLINAE, and only three pairs in ASCODIPTERINAE. The first pair of spiracles of the NYCTERIBOSCINAE is lost, and, therefore, their apparent 6th pair is homologous to the 7th of the other Diptera.

The 7th pair of spiracles of the NYCTERIBOSCINAE (fig. 1 A, and B, 7*sp*) enables us to determine the homology of the most anterior sclerites of the posterior part of the abdomen of the female. As each of these sclerites lies postero-dorsally to the 7th spiracles, they represent the parts of the 7th tergite (7t). In some species of this subfamily the number of the abdominal segments, between the 2nd and the 7th segment, can be determined by the number of long setae which occur on each side of the bare part of the abdomen. These setae are the remains of the vanished tergites, and their number corresponds to that of the spiracles above which they are situated. Thus, in *Nycteribosca gigantea* there are four pairs of one or two long setae between the 2nd tergite and the lateral part of the 7th tergite, and they represent the remains of the setae of the 3rd-6th tergites. The two long setae of the 6th tergite are seen

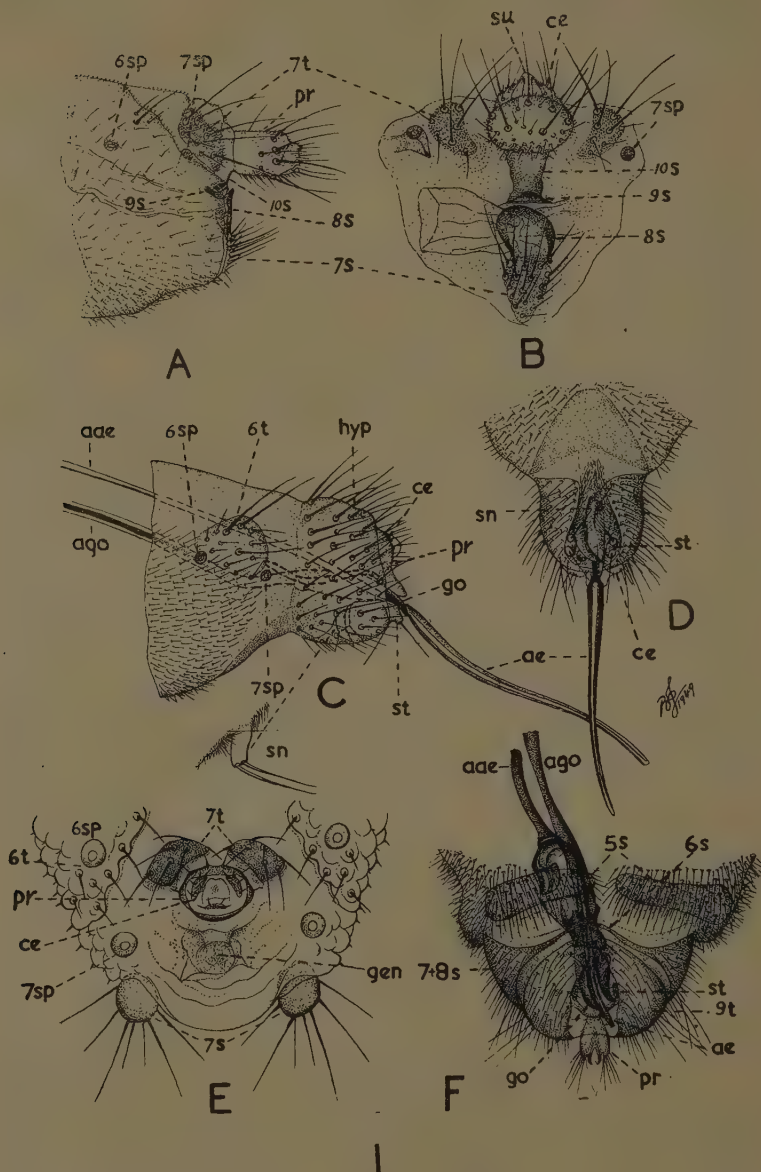


FIG. 1.—*Nycteribosca gigantea* Speiser. A, lateral and B, posterior view of end of abdomen of female; C, lateral and D, ventral view of same of male; E, ventral view of posterior end of abdomen of *Aspidoptera megastigma* Speiser; F, same of *Trichobius major* Coquillett. For explanation of lettering see p. 246.

in drawing 1 A, postero-dorsally to the 6th abdominal spiracle. The sclerites of the 7th tergite and their chaetotaxy are different in the species of the genus *Nycteribosca*, and therefore they are important taxonomically.

The 7th sternite (7s) is more or less closely united with the 8th sternite (8s), and, owing to the distension of the posterior part of the abdomen in these flies, it has become shifted posteriorly into the vertical position (fig. 1 A). The 8th and 9th tergites are absent. The 8th sternite is an irregular rounded plate, which projects dorsally under the proctiger and closes the genital opening. Above the 8th sternite there is a very small curved plate, which is movably attached to the 10th sternite and probably represents the 9th sternite (9s). It projects anteriorly and forms a part of the dorsal wall of the atrium which leads into the genital opening.

The proctiger (*pr*) is almost entirely formed by the 10th abdominal segment. Its form varies in the species of the NYCTERIBOSCINAE. It usually bears four dorsal, two lateral and two ventral long setae. Owing to the disappearance of the 11th segment the cerci (*ce*) are attached to the postero-lateral parts of the 10th segment (fig. 1 B and 6 E). Between them and a small conical ventral plate is located the anus. The ventral plate is very thin and projects posteriorly as far as or slightly beyond the cerci. It is the subanal plate of Crampton (*su*), and is probably homologous to the structure which Snodgrass (1935) called the hypoproct in the lower insects.

The female abdomen of the TRICHOBIINAE and the STREBLINAE differs from that of the NYCTERIBOSCINAE in several details. Their first two abdominal segments are more sclerotized, and in some genera the 2nd sternite is very large, forming one-third of the ventral surface of the abdomen. In *Trichobius caecus*, *T. parasiticus*, and especially in *Euctenodes mirabilis*, the abdominal segments 3-6 are indicated by narrow patches of setae, which extend from the ventral surface of the abdomen to the bare part of the dorsum (fig. 2 A). In *Aspidoptera megastigma* the tergites 3-6 have a festooned posterior margin (fig. 1 E), while in *Nycterophilia coxata* all the segments are strongly sclerotized. The 7th tergite of these two subfamilies is represented by a single small sclerite, or like that of the NYCTERIBOSCINAE, by two sclerites. The 7th sternite in all of them is divided mesally into two rounded sclerites, which usually project beyond the posterior margin of the abdomen and bear long setae. Their 8th and 9th sternites are absent, so that the margin of the genital opening (*gen*) is entirely membranous and is not very distinct in cleared specimens (fig. 1 E). The proctiger is usually small, but much more sclerotized than that of the NYCTERIBOSCINAE. In *Trichobius major* and *T. corynorhini* the proctiger is strongly sclerotized and darkly pigmented. Its posterior tergal and sternal parts are strongly produced, forming slightly convex plates. The cerci of these two species are very long, flat, and lie laterally to the posterior plates of the proctiger.

The abdomen of the ASCODIPTERINAE was described in my two previous papers (Jobling, 1939 and 1940). To this description it is necessary to add that the three pairs of abdominal spiracles of this subfamily belong to the 5th, the 6th and the 7th abdominal segments respectively. This has been established by an examination of the position of the spiracles in the abdomen of the male, in which the segments of the abdomen are more or less discernible. The other structures which have not been homologized in those two papers are the cerci. They are ring-shaped, and lie dorsally to the slit-like aperture

of a shallow pocket-shaped chamber, into which open the narrow rectum and the broad vagina.

The disappearance of the sclerites in the greatest part of the abdomen of the female and the splitting of the tergite and the sternite of the 7th segment is connected with the method of reproduction in these flies. These changes in the structure facilitate a very considerable distension of the abdomen during the growth of the larva, and also the expulsion of the latter from the uterus. The process of reproduction was briefly described in *Aspidoptera clovisi* (Jobling, 1949b), but it has not yet been studied in live specimens.

The Male Abdomen.

In the STREBLIDAE, as in many other Diptera, the male abdomen can easily be separated into the preabdomen and the postabdomen of Metcalf (1921), because the parts so named are structurally quite distinct from each other. The preabdomen is the largest and broadest part which extends posteriorly as far as the narrow membranous part which separates it from the postabdomen. The postabdomen is the most posterior part, which consists of the sclerotized hypopygium, the proctiger and the genitalia. In the male abdomen of the NYCTERIBOSCINAE all the abdominal spiracles are found in the preabdomen, while in the TRICHOBIINAE and the STREBLINAE the 7th pair of spiracles (7*sp*) is located in the postabdomen (fig. 2 A).

In the most posterior part of the preabdomen of the NYCTERIBOSCINAE there are present two small sclerites (fig. 1 c). However, these sclerites do not belong to the part of the 7th tergite, as those of the female. They lie postero-dorsally to the 6th abdominal spiracles (6*sp*), and therefore represent parts of the 6th tergite (6*t*). In this subfamily the sternite of the 6th segment is absent. In some species of the genus *Nycteribosca* there is a slightly sclerotized area in the ventral part, near the hypopygium, which resembles the sternite (fig. 1 c and d). But it is devoid of any cuticular appendages, and is considered here as a secondary structure.

The posterior part of the preabdomen of the TRICHOBIINAE and the STREBLINAE differs structurally from that of the NYCTERIBOSCINAE (fig. 1 f). Its postero-ventral part ends in two sclerites, which represent parts of the 5th sternite (5*s*). Their 6th tergite is absent, but its position is shown by a group of setae among which is seen the 6th abdominal spiracle (fig. 2 A, 6*sp*). Their 6th sternite, like that of the other Calypterae, is fused with the sternite of the 7th segment, as will be shown presently.

The most conspicuous part of the postabdomen is the large sclerotized hypopygium. In the TRICHOBIINAE and the STREBLINAE it consists of the large anterior synsternite, which is formed by the union of the 6th, 7th and 8th sternites, and the posterior semispherical part, which is the 9th tergite (9*t*). It is quite possible that a part of the 7th tergite enters into the composition of the synsternite, because the 7th abdominal spiracles (7*sp*) are present in its lateral parts, not far from the anterior margin (fig. 2 A). In *Aspidoptera* and *Paradyschiria* the synsternite and the 9th tergite are completely fused together, forming the strongly sclerotized semispherical hypopygium. In the other genera of these two subfamilies the process of fusion of these two sclerites shows a very considerable variation.

The hypopygium of the NYCTERIBOSCINAE consists of a single arch-shaped sclerite, which is probably formed by the 8th sternite and the 9th

tergite only, because their 7th abdominal spiracles lie near the postero-ventral margin of the 6th tergite, and are separated from the hypopygium by a very wide membrane (fig. 1 c).

In order to understand the homology of the sclerites which form the hypopygium, it is necessary to mention here that the postabdomen of STREBLIDAE undergoes a process of torsion, during which the 7th, 8th and 9th segments

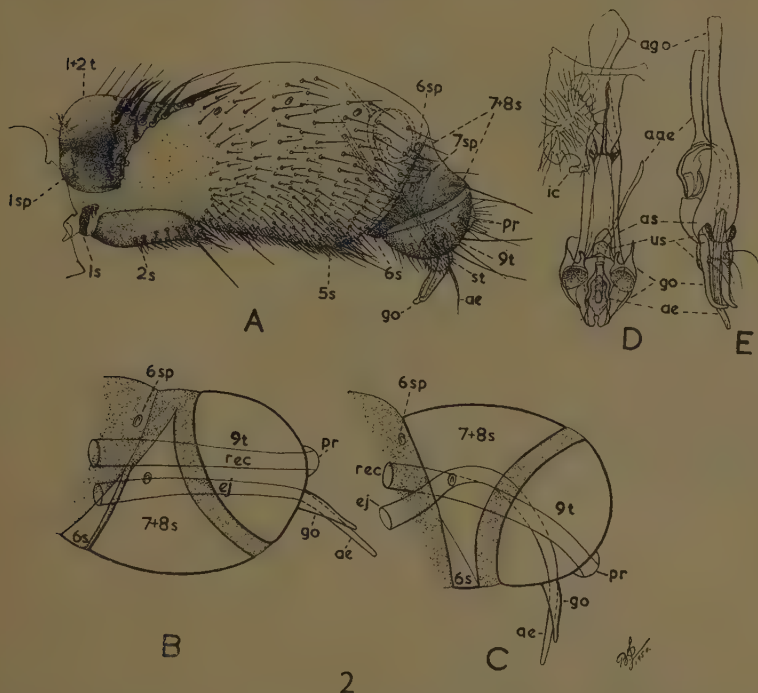


FIG. 2.—A, lateral view of abdomen of *Euctenodes mirabilis* Waterhouse; B and C, diagram showing posterior segments of abdomen before and after torsion; D, ventral view of 9th sternite of *Glossina palpalis* R. D.; E, same of *Trichobius major* Coquillett. For explanation of lettering see p. 246.

rotate round the longitudinal body axis from left to right. The rotation was observed in *Calliphora* by Schröder (1927); in the other Cyclorrhapha by Crampton (1941); and more recently it has been discussed by Hardy (1944). The rotation of the postabdomen of the STREBLIDAE has been established by dissection of the abdomen of *Raymondia planiceps*. It has been found that the ejaculatory duct of this fly is looped over the rectum from left to right. It has also been found that in some specimens of the TRICHOBIINAE the 6th sternite is somewhat assymmetrically fused with the 7th sternite.

The process of rotation and the changes in the position of the tergites and the sternites probably occur as shown in the diagram (fig. 2 B and C). During

this process the 9th segment is completely circumverted, so that its tergite (9*t*) takes again the same position. The synsternite (7 + 8*s*) rotates 180°, and as it moves into the dorsal position its posteriorly projecting part presses against the 9th tergite and swings it parallel to the sagittal plane of the body. Thus, the 9th segment rotates about two planes which are at right angles to each other. After rotation the 6th sternite (6*s*) unites with the synsternite, and closes the gap between the latero-ventral parts of the latter. In some specimens of *Euctenodes mirabilis* the sutures produced by this fusion are distinct as very thin lines. But they are not visible when the specimen is examined laterally because the 6th sternite is completely ventral and is curved inwards. In some species of *Trichobius* the part formed by the 6th sternite is very thin (fig. 1 F), while in others it is completely obliterated.

After rotation the genitalia become directed antero-ventrally under the abdomen as those of the other Cyclorrhapha, in which the male takes the position on the back of the female during mating. The permanent rotation of the segments of the postabdomen is an adaptation which changes the position of the male intromittent organ in such a way that it is easily brought in conjunction with the female genital opening. In the higher Diptera these modifications have been fixed genetically after the male acquired the habit of taking the above-mentioned position during mating.

The proctiger of the male is composed of the same parts as that of the female but is much smaller, and lies nearer to the postero-dorsal margin of the 9th tergite. Although I have not detected any sign of twisting in the rectum, it is quite possible that the proctiger follows the rotation of the 9th segment. The cerci of the male are very small, and in many species are completely fused with the 10th segment. In some species they bear comparatively long setae, while in others their setae are very short.

The Appendages of the 9th Tergite.

Below the proctiger the membranous cuticle forms a pocket, from which protrude the aedeagus (*ae*) and the gonapophyses (*go*). On each side of this pocket and close to the inner margin of the 9th tergite there are present small sclerites, the surstyli (*st*). They occupy the same position as those of *Glossina*, in which genus they were called the edita by Newstead (1911). They are appendages of the 9th tergite, and are probably sensory in function. In the genus *Nycteribosca* each surstylus is quite distinct and bears two long setae (fig. 1 C and D). They are absent in *Raymondia*, while in the TRICHOBIINAE and the STREBLINAE they have many small setae (fig. 1 F and fig. 2 A).

The 9th Sternite and the Genitalia.

Anteriorly to the pocket, the membranous cuticle of the NYCTERIBOSCINAE has two more or less cylindrical sclerites (*sn*), which are similar in form to the surstyli and also bear two long setae (fig. 1 C and D). Their position with regard to the other parts of the 9th sternite is as that of the inferior claspers of *Glossina*, and, therefore, they are considered here as the same. In *Raymondia* these sclerites are rather long and lie completely outside. In *Nycteribosca* they are concealed in the depressed part of the membrane, between the ventral margins of the 9th tergite, while in the two subfamilies of the American

STREBLIDAE they are absent. Their function is probably the same as that of the surstyli.

The 9th sternite of the STREBLIDAE, like that of many other higher Diptera, is greatly modified, and is withdrawn inside the segments forming the post-abdomen. The traces of withdrawal are seen externally in *Glossina* (fig. 2 D), where the cuticle between the inferior claspers (*ic*) is bent inwards, forming darkly pigmented folds which look more or less like an inverted T. In the STREBLIDAE the 9th sternite is trough-shaped, and is called here, as in *Glossina*, the aedeagal sheath (fig. 2 E, *as*). Its anterior part, as that of *Glossina*, is produced into the apodeme of the gonapophyses (*ago*), or the hypandrial apodeme of Crampton (1942), while its posterior broad part is forked and bears the gonapophyses (*go*). Ventrally and dorsally to the basal parts of the gonapophyses there are attached to the aedeagal sheath the U-shaped sclerites (*us*), of which the ventral one is homologous to that of *Glossina*. To these sclerites and to the lateral margin of the forked part of the sheath is attached the inverted membrane which forms the pocket around the external parts of the genitalia. The U-shaped sclerites are absent in the NYCTERIBOSCINAE. In species of the genus *Nycteribosca* there is present a zigzag curved sclerite, which is shown in fig. 1 C by dotted lines. It has an asymmetrical position at the side of the 9th sternite and is not attached to the genitalia. It probably represents the greatly modified sclerite, which in the American STREBLIDAE lies between the postero-dorsal margin of the aedeagal sheath and the curved backwards anterior end of the aedeagus (fig. 2 E).

The term "gonapophysis" was introduced by Lowne (1893-95). In my previous papers the gonapophyses were called the claspers. Patton and Cushing (1934), and Patton (1934), called them parameres. Crampton used the terminology of Lowne, and considered them as homologous to the inferior claspers of *Glossina*. But the inferior claspers in this genus have a connection with the aedeagal sheath different from that of the gonapophyses, and therefore it seems to me that in the higher Diptera they have been derived from the other parts than the inferior claspers. Hardy regards them in *Muscoidea* as parts of the 8th tergite, while the 9th sternite he calls the apodeme of this tergite.

In order to understand the origin of the gonapophyses, it is necessary to consider the position of the aedeagus in the aedeagal sheath and the sclerites of the posterior part of the latter. During the present study the parts in question have been compared with those of *Glossina*, because in the species of this genus the aedeagus and its sheath are less modified than those of other higher Diptera. The aedeagal apodeme of *Glossina* (fig. 2 D) lies dorsally to the sheath. Its proximal end is movably attached to the dorso-posterior end of the latter, where it is also connected with the ejaculatory duct. From this point the ejaculatory duct bends ventrally and opens in the middle of the aedeagus (*ae*). The latter lies postero-ventrally to the anterior forked part of the sheath and between the sclerites which were called by Newstead the harpes. In the STREBLIDAE the aedeagal apodeme is also dorsal to the sheath, but owing to the elongation of the aedeagus it lies above the apodeme of the gonapophyses (fig. 2 E). The anterior half of the aedeagus lies in the dorsal concave part of the sheath, while its posterior half protrudes through the arch formed by the forked part and lies between the gonapophyses. It is seen in the drawing that the gonapophyses have the same relation to the

forked part of the sheath and the aedeagus as the harpes of *Glossina*, and therefore it is more likely that they have been derived from the processes of the posterior part of the aedeagal sheath. Their position also indicates their homology to the anterior gonapophyses of the higher Diptera.

The structure of the gonapophyses varies considerably in the subfamilies of the STREBLIDAE. Thus, in the TRICHOBIINAE and the STREBLINAE they are of equal length, and each of them bears either two long or a few short setae. In the species of the genus *Nycteribosca* the left gonapophysis is slightly shorter than the right one, while in *Raymondia* the left gonapophysis is almost completely obliterated.

The structure of the abdomen of the NYCTERIBOSCINAE differs considerably from that of the TRICHOBIINAE and the STREBLINAE, as shown below in the summarized form.

NYCTERIBOSCINAE.	TRICHOBIINAE and STREBLINAE.
<i>Female.</i>	<i>Female.</i>
1st abdominal spiracles absent.	1st abdominal spiracles present.
7th sternite not divided.	7th sternite divided.
8th and 9th sternite ? present.	8th and 9th sternite absent.
Proctiger large.	Proctiger usually very small.
<i>Male.</i>	<i>Male.</i>
6th tergite present and divided.	6th tergite absent.
5th sternite absent.	5th sternite present and divided.
8th sternite and 9th tergite completely fused.	Synsternite 7 + 8 and 9th tergite usually distinct.
7th spiracles in preabdomen.	7th spiracles in synsternite 7 + 8.
Appendages of 9th sternite present.	Appendages of 9th sternite absent.
Left gonapophysis reduced or almost obliterated.	Gonapophyses of equal length.
Apodemes of genitalia very long and thin.	Apodemes of genitalia short and thick.

This difference, together with that of the head, the thorax and the wings (Jobling 1936a), seems to indicate that the American STREBLIDAE and the NYCTERIBOSCINAE of the Old World, though related, have been derived from different ancestral forms. But owing to the adaptation to the same environmental conditions, both groups acquired several characters which have no relation to their phylogeny. The ancestral forms of these two groups belonged to the Calyptræ, because the present members of this section of Diptera and the STREBLIDAE have the following common characters: The presence of the thoracic calli and the position of the squamae; the very well-developed internal ridges in the syntergite 1 + 2; the position of the abdominal spiracles in the tergites or in the tergal parts of the segments; the free 6th tergite; and the position of the 7th abdominal spiracles in the synsternite 7 + 8. Besides these characters, the aedeagus, its sheath and the gonapophyses are also of importance, because their structure and position resembles those of the Calyptræ rather than the Acalyptræ.

HOST-PARASITE RELATIONSHIP AND GEOGRAPHICAL DISTRIBUTION.

In my previous paper (1949a) the relationship of the American STREBLIDAE to their hosts was described at some length. It was shown that the roosting

habit of bats has been an important factor in the adaptation of these flies to the different species of bats. According to this habit the species of Old World bats can be separated into two groups: (1) Those which roost in different places from the other species. To this group belong *Lyrioderma lyra lyra* (Geoffroy), *Cynopterus brachyotis brachyotis* S. Müll. (= *C. brachyotis lusoniense* Peters), and probably some other species mentioned in the table, but of which the roosting habit is not known. (2) This group includes all those species which roost in caves, where some of them hang close together, either in small or large batches, while others form loose assemblages, in which individual bats roost more or less apart from each other. Owing to the isolation of the bats in the first group, they are neither infested with the STREBLIDAE of the other bats nor pass their own parasites to them. The STREBLIDAE which parasitize these bats are usually monoxenous, and have the same geographical distribution as their specific hosts. To the monoxenous STREBLIDAE belong *Nycteribosca scutellaris* Jobling, *N. buxtoni* Falcoz, *N. rouxi* Falcoz, and *Raymondia lobulata* Speiser. The distribution of the first two species closely corresponds to that of their host, *Emballonura semicaudata* (Peal), which inhabits the two groups of islands, Fiji and Samoa; *N. rouxi*, as its host, *Notopteris neocaledonica* Troussart, is restricted to New Caledonia, and *R. lobulata* follows the distribution of *Lyrioderma lyra lyra* (Geoffroy), which inhabits Ceylon, India and South China.

The host-parasite relationship of *N. cucullata* Jobling shows an interesting exception from that of the species just mentioned. It parasitizes two species of bats which have different roosting habits. Its principal host is *Taphozous melanopogon melanopogon* Tem., which according to Phillips (1922) roosts in a large colony, in crevices and fissures of masses of rocks and boulders overhanging brush wood. But this Streblid has also been recorded from *Cynopterus brachyotis brachyotis* S. Müll., which, according to the author just mentioned (1924), is an arboreal bat, roosting in palms. The occurrence of *N. cucullata* on *C. brachyotis brachyotis* shows that this bat may occasionally roost in the same place or more or less close to a colony of *T. melanopogon melanopogon*, or vice versa, and thus acquires this parasite. Apparently the same relationship exists between these two bats and *N. hoogstraali* sp. n. STREBLIDAE are mostly parasites of cave bats; only a very few arboreal bats have them. The latter probably more often acquire them through some other bat; which has no fixed roosting habit, and may spend the night either in a cave or in the open among the trees, as, for instance, *Artibeus jamaicensis jamaicensis* Leach of the New World. It seems that *T. melanopogon melanopogon* also belongs to this class of bat.

The bats of the second group, owing to their habit of roosting in the confined space of the cave, are easily infested with STREBLIDAE, and therefore each single species may harbour several species and genera of these ectoparasitic flies. Thus, *Taplozous melanopogon philippinensis* Waterhouse and *Miniopterus australis australis* Tomes are parasitized each by three species of the genus *Nycteribosca*; and *Rhinolophus blythi blythi* Andersen by one species of *Nycteribosca* and by two species of *Raymondia*.

According to the present record, seven species of bats belonging to five genera have been found in a single cave in the Philippines. As all these bats roost in large numbers they create in the cave very favourable conditions for the adaptation of many species of STREBLIDAE to bats belonging to different

TABLE I--(cont.).

[illegible]

Microchiroptera.

genera and families of Chiroptera. For example, *Nycteribosca gigantea* Speiser parasitizes five species of the PTEROPIDAE, one of the HIPPOSIDERIDAE and one species of the VESPERTILIONIDAE; *N. amboinensis*, one species of the PTEROPIDAE, one of the HIPPOSIDERIDAE and six species of the VESPERTILIONIDAE; and *Raymondia pseudopagodarum* sp. n. one species of the PTEROPIDAE, three of the RHINOLOPHIDAE, one of the HIPPOSIDERIDAE and one species of the VESPERTILIONIDAE. (The records of this species indicated by letters b and c in Table I are not included here.) However, these STREBLIDAE do not occur in the same degree on all these bats, but show a definite preference for certain species or genera, which must be regarded as their principal hosts. Thus, *N. gigantea* is more common on the genus *Dobsonia* and the *Eonycteris*, which belong to the same family of Chiroptera; *N. amboinensis* on the genus *Miniopterus*, especially on *M. schreibersi blepotis* (Temminck) and its subspecies; *N. modesta* and *R. pseudopagodarum* on the genus *Rhinolophus*; and *R. pagodarum*, on the genus *Hipposideros*.

Owing to the adaptation of the heteroxenous STREBLIDAE to different hosts, their geographical distribution is much wider than that of the monoxenous STREBLIDAE. The distribution of *N. gigantea* extends from the Philippines to Java and to the Solomon Islands; of *R. pagodarum*, from Ceylon through India to Burma, and then to New Guinea, and to Sumba Island; of *R. pseudopagodarum*, from South China to Malay Peninsula and to the Philippines. *N. amboinensis* has the widest distribution. It is present in almost all parts of the Oriental Region, and in the Australian Region it occurs in New Caledonia, Queensland, and in New South Wales. It has also been found in Okinawa, Riu-Kin Islands, which belong to the Palaearctic Region.

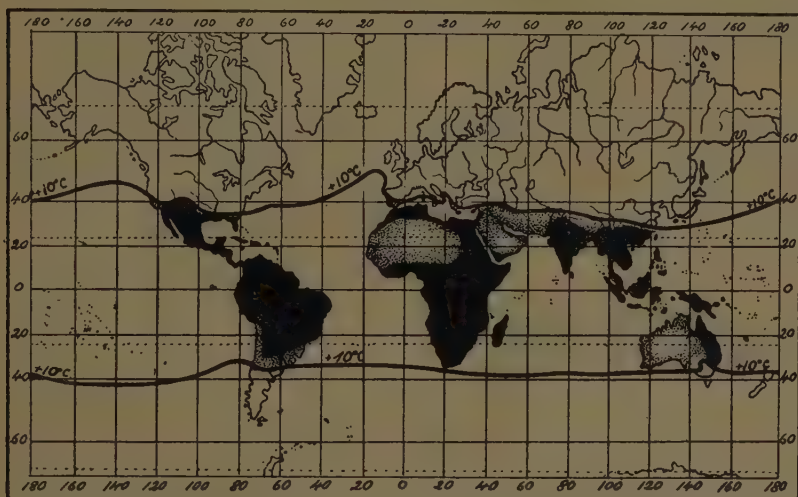
According to the distribution of these STREBLIDAE in the two geographical regions, they may be roughly grouped as follows: (1) Oriental Region: *N. nigriceps*, *N. cucullata*, *N. macrops*, *N. speiseri*, *N. hoogstraali*, *N. falconi*, *N. modesta*, *N. proxima*, *N. werneri*, *N. pygialis*, *N. caudata*, *R. lobulata*, *R. pseudopagodarum* and *R. javanica*. (2) Australian Region: *N. pretosa*, *N. surcoufi*, *N. franclemonti*, *N. minuta*, *N. scutellaris*, *N. rouxi* and *N. buxtoni*. (3) Oriental and Australian Regions: *N. gigantea* and *R. pagodarum*. (4) Palaearctic, Oriental and Australian Regions: *N. amboinensis*.

None of these STREBLIDAE occur in the Ethiopian and in the Mediterranean parts of the Palaearctic Regions, and vice versa. It is quite possible that the distribution of the Oriental species westwards and the Mediterranean species eastwards is prevented by climatic conditions which are present in winter on the Iranian Plateau, especially on its central range, which extends from Azerbaijan to Baluchistan. Owing to the elevation and the prevailing cold north-easterly wind, the temperature of this part of the Plateau is too low for bats to survive the winter without hibernation. Further east, on the Paropamisus range and Hindu Kush, the winter is much more severe than on the Central range.

As the STREBLIDAE are pre-eminently tropical flies, in which the generations succeed one another all the year, they cannot exist on hibernating bats. The body temperature of the hibernating bats, as investigated by Burbank and Young (1934) in England, and Eisentraut (1934) in Germany, is only a fraction of a degree above that of their environment, while the critical temperature at which the bats begin to hibernate is about $+10^{\circ}\text{C}$. (Eisentraut). Even during their daily sleep in summer their body temperature is equal to or only

a few degrees above that of the surrounding air. It has been observed by Allen (1939) that the big brown bats begin to leave their hibernating places near Boston in spring, when the temperature of the air is about $+12^{\circ}\text{C}$. My own observations on *Pipistrellus pipistrellus* Schreiber show that this bat may come out in December, if the day and the evening temperature is about 12.5° and 11.5° respectively, but only when the temperature of the previous night was not less than $+10^{\circ}\text{C}$.

As the STREBLIDAE cannot exist on hibernating bats, they are present only in those parts of the world where their hosts are active all the year round. This is in agreement with their general geographical distribution, as shown in Map I. In both hemispheres they do not occur beyond the winter isotherm



MAP I.—Showing the distribution of STREBLIDAE and the winter isotherms of $+10^{\circ}\text{C}$. Stippled areas indicate where they may be found in future.

of $+10^{\circ}\text{C}$., that is the critical temperature below which their hosts begin to hibernate. They also do not follow their hosts beyond this isotherm. For instance, *Rhinolophus hipposideros* Bechstein and *R. ferrum equinum* Schreiber are present in Central Europe and in England, and *Miniopterus schreibersi schreibersi* Kuhl in Switzerland and Hungary, but their Streblid, *Nycteribosca africana* Walker, does not occur in these parts of Europe (Map II). There are only two records of this species north of the January isotherm of $+10^{\circ}\text{C}$., one from *Rhinolophus ferrum-equinum*, in southern France (Falcoz, 1926), and another from an unknown species of bat, near Askobad, in Turkistan.* As regards the first record, it is quite possible that the bat came from a more southern locality and brought the parasite with him, because it is known that in the south of France *R. ferrum-equinum* shows periodic migration (Hugues, 1913). *N. africana* may undoubtedly occur in some

* For this last record I am very grateful to Dr. A. A. Stackelberg of the Zoological Institute of the Russian Academy of Science.

warm localities which lie north to the January isotherm of $+10^{\circ}\text{C}$., or temporarily survive after an exceptionally warm winter. The absence of this species from southern Spain, Sicily and Crete is more probably due to lack of examination of the bats for this fly than to any other ecological factor, because all these countries lie to the south of the above-mentioned isotherm.



MAP. II.—Showing the distribution of *Nycteribosca africana* Walker in the Mediterranean parts of the Palaearctic region, the northern limit of the distribution of its hosts, and the January isotherm of $+10^{\circ}\text{C}$. Stippled areas indicate where this species may be found in future.

Rhinolophus hipposideros Bechstein, ● — ● — ● — ●

R. ferrum-equinum Schreiber, ●● — ●● — ●●

Miniopterus schreibersi schreibersi Kuhl, × × × × ×

Genus *Nycteribosca* Speiser, 1900.

Head broad in its anterior part, becoming narrow towards occipital foramen, its dorsal and ventral surfaces convex; no depressions for the fore-coxae. One-faceted eyes present; postvertex (vertical triangle) distinct. Arista of antennae flagelliform, with a few branches in its distal half. Palpi usually longer than broad, with rounded distal margin. Thorax almost spherical, with very distinct, complete mesonotal suture; humeral calli absent; scutellum with many setae usually of variable number and size. Wings more than twice as long as broad, with five longitudinal veins; 1st longitudinal vein not much thicker than the 2nd, with setae in its distal part only; numerous setae in humeral and costal cells, those near costal margin and in humeral cell distinctly longer; alula well developed and fringed with setae.

Since the genotype was not indicated by Speiser (1900) I selected *Strebla africana* Walker, 1849. It is the first described species, common and widely distributed in the Ethiopian region and in the Mediterranean parts of the Palaearctic region.

Key to the Species of the Genus *Nycteribosca* of the Oriental and the Australian Regions.

1. Posterior part of the thoracic squamae broadly rounded (figs. 3 c and 4 A) 2.
Posterior part of the thoracic squamae conical (figs. 6 A, B, c and 7 A) 9.
2. Head very much darker than body 3.
Head not darker than body 6.
3. Postvertex small, elliptical. Flies 3 mm. 4.
Postvertex large, circular or deltoid. Flies less than 2 mm. 5.
4. Labella (*l*) as long as or a little longer than the theca (*t*). Distal part of the 1st basal cell widened, with divergent sides (figs. 6 G and H) *N. gigantea* Speiser.
Labella very much shorter than the theca. Distal half of 1st basal cell oblong, with parallel sides (fig. 6 F) *N. nigriceps* Jobling.
5. Postvertex deltoid, attached to the occiput. Theca of labium rounded. Apodemes of the male genitalia about one-third of the length of abdomen *N. cucullata* Jobling.
Postvertex almost circular, separated from the occiput. Theca of labium subconical. Apodemes of the male genitalia two-thirds of the length of abdomen; that of the aedeagus extends to the anterior end of abdomen (figs. 4 A, B and C) *N. macrops* sp. n.
6. 3rd and 4th longitudinal veins divergent near the wing margin 7.
3rd and 4th longitudinal veins parallel, or the 3rd slightly bends away from the 4th near the wing margin 8.
7. Postvertex elliptical, with two setae. Anterior part of theca of labium conical (fig. 3 A) *N. scutellaris* Jobling.
Postvertex cuneate, with rounded anterior margin. Anterior part of theca of labium rounded (fig. 3 B) *N. buxtoni* Falcoz.
8. Post vertex circular, defined by setae, with indistinct margin. Posterior margin of scutellum rounded (fig. 3 c) *N. speiseri* Jobling.
Postvertex elliptical, very distinct. Posterior margin of scutellum pointed (fig. 5) *N. hoogstraali* sp. n.
9. 3rd and 4th longitudinal veins divergent near wing margin 10.
3rd and 4th longitudinal veins parallel near wing margin 19.
10. Posterior part of scutellum with darkly pigmented, pointed process (fig. 3 D) *N. rouxi* Falcoz.
Scutellum without process 11.
11. Basal part of 3rd longitudinal vein longer than anterior cross-vein. Pleurotrochantines slightly more setose than the sternopleura (fig. 3 E and F) *N. falcozi* Jobling.
Basal part of 3rd longitudinal vein as long as or shorter than anterior cross-vein. Sternopleura and pleurotrochantines uniformly setose 12.
12. Thorax as long as or a little longer than broad. Proctiger conical (fig. 6 E) 13.
Thorax broader than long. Proctiger not conical 15.
13. Postero-dorsal part of head bombiform. Middle part of the anterior margin of sternopleura almost straight (fig. 3 J) *N. surcoufi* Falcoz.
Postero-dorsal part of head not bombiform. Middle part of the anterior margin of sternopleura distinctly or indistinctly bilobed (fig. 3 I) 14.
14. Scutellum rounded or slightly triangular (fig. 6 A and D) *N. amboinensis* Rondani.

- Scutellum distinctly triangular (fig. 6 B) *N. pretiosa* Falcoz
15. Postvertex circular. Scutellum triangular (fig. 3 a) *N. franclemonti* Matheson.
 Postvertex not circular. Scutellum broadly rounded 16.
 16. Distal part of 1st longitudinal vein strongly bent towards costa 17.
 Distal part of 1st longitudinal vein gently bent towards costa 18.
 17. Mediovertex narrow; postvertex elliptical, separated from occiput.
 Postero-ventral part of abdomen of female with a row of curved,
 darkly pigmented spines (fig. 3 H) *N. minuta* Jobling.
 Mediovertex broad; postvertex cochleariform, fused with occiput.
 Abdomen of female without spines (fig. 7) *N. proxima* sp. n.
 18. Postvertex cochleariform. Femora very thick and setose (fig. 3 K,
 L and M) *N. modesta* Jobling.
 Postvertex cordiform. Femora neither very thick nor very setose
 (fig. 8) *N. werneri* sp. n.
 19. Postvertex circular. Proctiger with six dorsal, two lateral and
 two ventral long setae (fig. 3 N) *N. pygialis* Jobling.
 Postvertex cordiform. Proctiger with seven dorsal, two lateral and
 four ventral long setae (fig. 3 O) *N. caudata* Jobling

Genus *Raymondia* Frauenfeld, 1855.

The definition of the genus has already been published by me in my paper on the African STREBLIDAE (Jobling, 1939), and it is reproduced here with some slight modification.

Head rounded laterally, as broad as the anterior part of thorax, or more or less quad-rangular and narrower than the thorax, dorso-ventrally flattened, closely articulated to the thorax, with concavity on each side of occipital foramen for the fore-coxae. Eyes absent. Postvertex (vertical triangle) absent. Arista of antennae short and thick, with many branches. Palpi nearly as long as broad, obtuse. Thorax somewhat flattened; mesonotal suture not well defined or incomplete in the middle; humeral calli very distinct; scutellum always with two very strong, long setae and a few small, usually marginal setae. Wings twice as long as broad, with five longitudinal veins; first longitudinal vein much thicker than the second vein, usually with setae along its entire length; few setae, or none in humeral and costal cells; alula not always well developed, without, or with one or a few setae.

Genotype *Raymondia huberi* Frauenfeld, 1855.

Key to the Species of the Genus *Raymondia* of the Oriental and the Australian Regions.

1. Transverse suture of mesonotum incomplete in the middle. Theca of labium broader than long 2.
 Transverse suture of mesonotum complete. Theca of labium as long as broad 3.
2. 4th longitudinal vein straight between the anterior and the posterior cross-veins. Alula with many setae. Each sternopleuron with oblong bare part (fig. 9 A and B) *R. lobulata* Speiser.
 4th longitudinal vein curved between the anterior and the posterior cross-veins. Alula with one terminal seta. Sternopleura uniformly setose *R. javanica* Falcoz.
3. Occiput with four to seven short, thick setae near the dorsal margin.
 Alula with one apical seta (fig. 9 c and p) *R. pagodarum* Speiser.
 Occiput without setae. Alula without apical seta (fig. 10) *R. pseudopagodarum* sp. n.

RECORD OF THE STREBLIDAE.

Surprisingly little has been known before of the STREBLIDAE of the Philippines. Only the following two species were recorded: *Nycteribosca gigantea* and *N. amboinensis*, both by Ferris (1924a and b). The present record includes nine species, of which five are described for the first time.

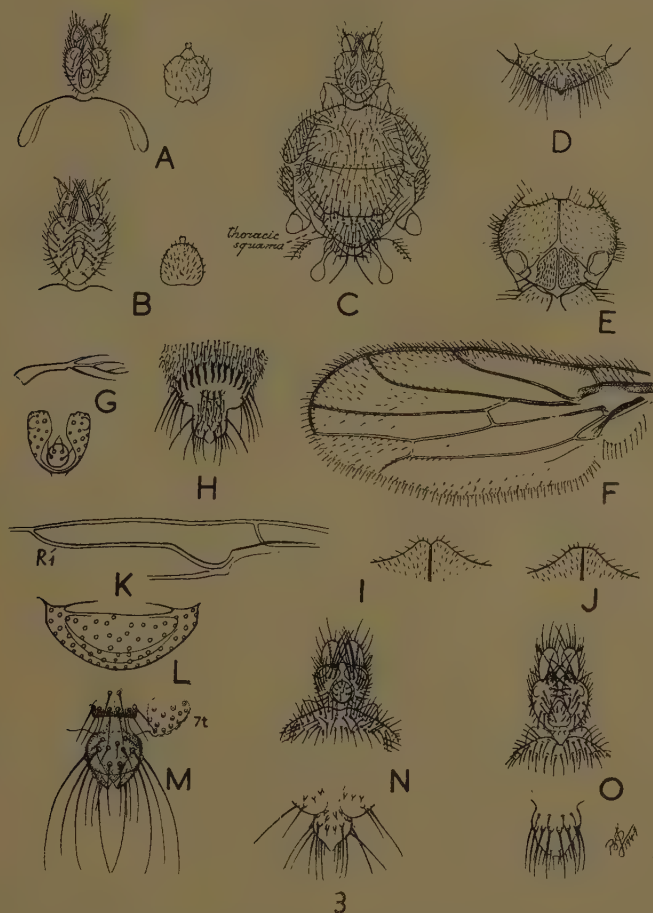


FIG. 3.—A, head and labium of *Nycteribosca scutellaris* Jobling; B, same of *N. buztoni* Falcoz; C, head and thorax of *N. speiseri* Jobling; D, scutellum of *N. rouxi* Falcoz; E, ventral view of thorax and F, wing of *N. falcozi* Jobling; G, vertex and arista of *N. franclemonti* Matheson; H, ventral view of posterior end of abdomen of *N. minuta* Jobling; I, anterior margin of sternopleura of *N. amboinensis* Rond; J, same of *N. surcoufi* Falcoz; K, 1st longitudinal vein of *N. modesta* Jobling; L, scutellum and M, proctiger of same; N, head and proctiger of *N. pygialis* Jobling; O, same of *N. caudata* Jobling.

Nycteribosca gigantea Speiser, 1900.

The type of this species was collected from *Dobsonia peroni* (Geoffroy), in Bismarck Archipelago. It has also been recorded from large Pteropid, in British Solomons; from *Cynopterus* sp., in Babakan, south coast of Java; from a bat, Bukidnar, Mindanao, P.I., from an unknown host, Montalban, Rizal Prov., Luzon, P.I., and from *Dobsonia sunbana* K.And., Sumba Island, 1913.

Present record: 2 specimens from a bag with *Miniopterus schreibersi bleoptis* (Temminck) and *Miniopterus australis australis* Tomes, Luang cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946; 30 specimens, Tawang Cave, Samal Island, Davao Prov., P.I., 2.xii.1946; 1 specimen in bag for collecting bats, Luangbay Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946; 1 specimen from bats' dung, same locality and date; 5 specimens from *Eonycteris spelaea glandifera* Lawrence, Tanabag, Puerto Princesa, Palawan Island, Palawan Prov., P.I., 17.iii.1947; 6 specimens either from *Rousettus amplexicaudatus* (Geoffroy) or from *Eonycteris spelaea glandifera* Lawrence, Luang Cave, Sitio Tegato, Davao City, Mindanao P.I., 22.x.1946; 22 specimens from *Hipposideros diadema griseus* Meyen, Central Cave, Cotabato City, Cotabato Prov., Mindanao, P.I., 26.xii.1946; 9 specimens, Luangbay Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.xii.1946; 16 specimens from *Eonycteris robusta* Miller, Central Cave, Cotabato City, Cotabato Prov., Mindanao, P.I., 27.xii.1946; and 4 specimens from Dilirig Prov., Bukidnar, Mindanao, P.I.

Nycteribosca cucullata Jobling, 1934a.

The type of this species was collected from *Taphozous melanopogon melanopogon* Temminck, Kalutara, Ceylon, 100 ft., by Capt. W. W. A. Phillips.

Present record: 2 specimens from *Taphozous melanopogon philippinensis* Waterhouse, Caburan, Davao Prov., Mindanao, P.I., 17.i.1947; 1 specimen from *Cynopterus brachyotis luzoniense* (Peters) = *C. brachyotis brachyotis* Müll., Malabutuan, Caburan, Davao Prov., Mindanao, P.I., 14.i.1947; and 4 specimens from *Taphos melanopogon philippinensis* Waterhouse, Malabutuan, Coburan, Davao Prov., Mindanao, P.I., 14.i.1947.

Nycteribosca macrops sp. n. (fig. 4).

This species resembles very much *N. cucullata*, from which, however, it can be easily separated by the characters mentioned in the key.

Body 1.9-2.1 mm. long (on slide) in male and female respectively. Head darker than the body; laterovertices with four or five long and a few short setae, mediovertex broad, distinct; postvertex almost circular, setose, separated from the occiput; a few small setae arise from the occiput behind the postvertex. Eyes large, projecting laterally beyond the lateral margin of the head. Ventral surface of head bears many small setae. Antennae and palpi presenting no distinctive character. Theca of labium subconical, narrower than that of *N. cucullata*; labella very short.

Thorax spherical, almost as long as broad, prescutum uniformly setose; scutum as long as prescutum, with two long setae arising from the middle and one from each lateral part; the rest of its surface bears the same setae as those arising from the prescutum; scutellum broadly rounded, with four very long, erect setae in the anterior part and a few much smaller setae in the posterior and the antero-lateral parts. Ventral surface of thorax bears very many small setae.

Wings 1.7-1.6 mm. long, narrow, with broadly rounded apex; 3rd and 4th longitudinal veins slightly divergent near the apex of the wings; setae of the costal and the marginal cells, like those of *N. cucullata*, crowded near the costal margin. Legs long; postero-dorsal part of the femora of the fore-leg and the antero-dorsal parts of the femora of the middle and the hind-leg with many strong setae.

Abdomen with two longitudinal rows of strong setae on its dorsal surface; proctiger small, with a row of six strong dorsal setae, and four long thin, and several very small ventral setae; 2nd sternite large, with small rather thick setae in the anterior half, and with many very fine small setae in the posterior half; the middle, setose part of the ventral surface separated from the 2nd sternite and the setose posterior end by bare parts; 7th sternite bears two long thin and a few very small setae.

Abdomen of the male narrower than that of the female; it ends in conical hypopygium. Apodemes of genitalia two-thirds of the length of abdomen; that of aedeagus extends to the anterior end of the abdomen.

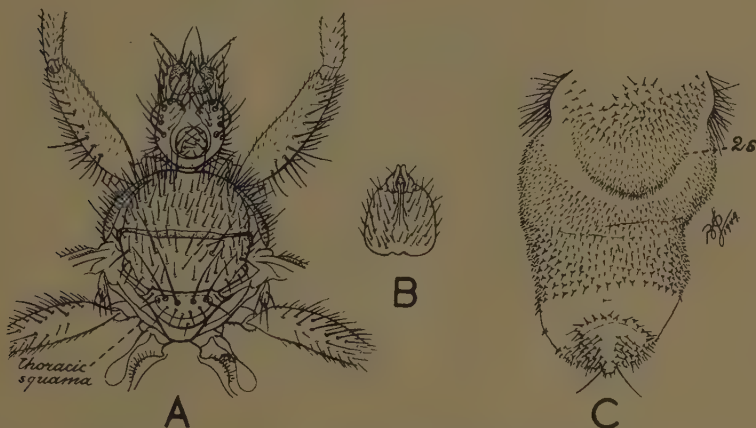


FIG. 4.—*Nycteribosca macrops* sp. n. A, head and thorax; B, labium; C, ventral view of abdomen of female. 2s, second sternite.

Three specimens were examined, two females and one male. They were collected from *Taphozous melanopogon philippinensis* Waterhouse, in Malabutuan, Caburan, Davao Prov., Mindanao, P.I., 14.i.1947. Holotype, female and allotype, male are preserved in the Chicago Natural History Museum. Paratype female is in the author's collection.

Nycteribosca scutellaris Jobling, 1936b.

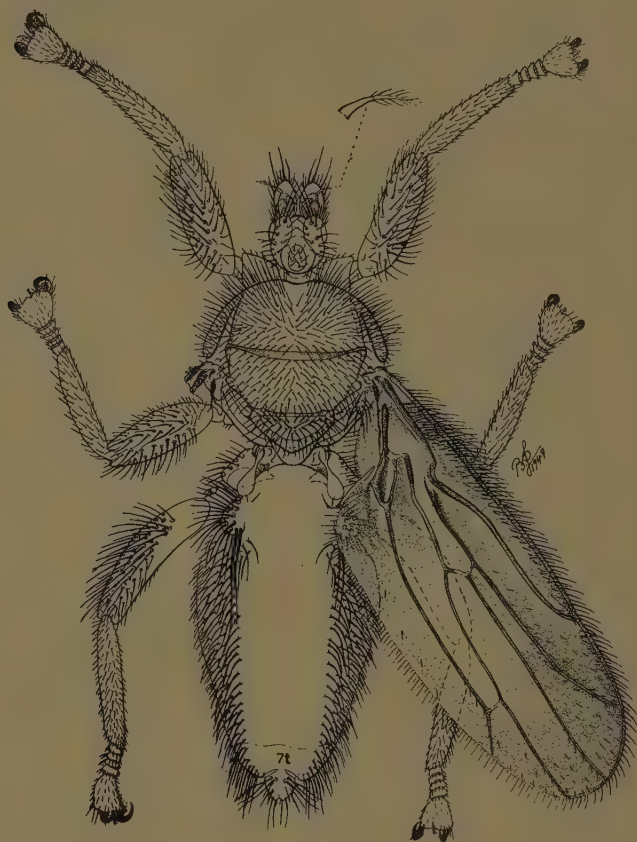
The only record of this species was the type, collected from *Emballonura semicaudata* (Peal), near Suva, Fiji Islands.

Present record: 4 specimens from a bat, 1 mile from Suva, Viti-Levu Island, Fiji Islands, 12.iii.1929, Crane Pacific Expedition.

Nycteribosca buxtoni Falcoz, 1927.

The type of this species was collected from *Emballonura semicaudata* Peale, in Malololelei, Upolu, Samoa. It has also been found on the same species of bat, in Waiga Gorge, Fiji Is., and on a bat, in Suva, 1929.

Present record : 3 specimens from a small bat, Viti-Levu, Fiji Is., 21 .iii. 1929, Crane Pacific Expedition.



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FIG. 5.—*Nycteribosca hoogstraali* sp. n. 7t, seventh tergite.

***Nycteribosca hoogstraali*, sp. n. (fig. 5).**

This species resembles *N. franclemonti* Matheson (1945), but belongs to that group in which the posterior part of the thoracic squamae is broadly rounded. It also differs from that species by the elliptical postvertex, larger eyes, the structure of the arista, which has many more branches than that of *N. franclemonti*, and by the structure of the wings.

Body 2.8 mm. long (on slide) in females. Head slightly more pigmented than the body; each laterovertex with three long setae in the anterior part and with much smaller setae, varying in length along the margin and in the lateral parts; mediovertex very broad;

postvertex elliptical, large, with small setae. Eyes large, slightly projecting beyond the lateral margin of the head. Ventral surface of head with long setae on the margin round the rostrum membrane, and with shorter setae behind and in the lateral parts. Palpi rounded, nearly as long as broad, with long setae in the anterior part of the ventral surface and much shorter setae along the margin and in the posterior part. Arista of antennae with many branches. Theca of labium rounded, as long as broad; labella very small.

Thorax slightly broader than long; prescutum with longer setae in the anterior than in the posterior part; scutum shorter than the prescutum, with setae of the same type as those arising from the posterior part of the prescutum; scutellum triangular, with longer setae in the middle than in the anterior and the posterior parts. Posterior part of the thoracic squamae broadly rounded. Ventral surface of thorax bears many small setae.

Wings 2.0 mm. long, narrow, with broadly rounded apex; 2nd longitudinal vein almost straight between the bend and the costa; 3rd longitudinal vein slightly bends away from the 4th near the wing margin; costal margin fringed with long setae; marginal, submarginal and posterior cells with a few setae; alula narrowly rounded and fringed with long setae. Legs moderately long, femora with many moderately strong setae.

Abdomen with many long setae on each side of the bare part of its dorsal surface; lobes of tergite 1 + 2 with two very long thick and many long thin setae; 2nd sternite with large triangular patch of small setae; parts of the 7th tergite large, with many long setae. Ventral surface bears numerous small setae. Prociger small, with two lateral and four dorsal long setae; its ventral surface, besides many small setae, bears four long thin ones in the posterior part.

The following specimens were examined: Type, female, from *Cynopterus brachyotis luzoniense* (Peters) = *Cynopterus brachyotis* S. Mül., and paratype, female, from *Taphozous melanopogon philippinensis* Waterhouse, collected in Malabutan, Caburan, Davao Prov., Mindanao, P.I., 14.i.1947. The types are preserved in the Chicago Natural History Museum.

Nycteribosca rouxi Falcoz, 1923.

The type of this species was collected from *Notopteris neocaledonia* Trouess., in New Caledonia.

Present record: 6 specimens from *Notopteris* sp., Poya, New Caledonia, 13.vi.1945.

Nycteribosca amboinensis (Rondani) Speiser, 1900.

Brachytarsina amboinensis Rondani, 1878

(fig. 6 A, C, D and E).

The examination of nearly 115 specimens shows that *N. amboinensis* is a very variable species. Almost all the specimens differ more or less from each other in their chaetotaxy, the structure of the head, the thorax and the wings. There is a distinct variation in the shape of the postvertex, which may be narrow, rather long and strongly acuminate, or more or less pyriform, with narrowly rounded anterior end. The thorax may be as long as or distinctly longer than broad, with broadly rounded or more or less triangular scutellum. But there is no correlation between the form of the thorax and that of the scutellum. The more or less triangular scutellum can be present in specimens with the long thorax and the rounded one in those of which the thorax is rounded. Fig. 6 D shows the variation of the scutellum of this species. The drawings (a) were made from specimens collected from *Miniopterus schreibersi*

blepotis (Temminck), in Amboina, which is the type locality of this species. I have examined seven specimens from Amboina, and have found that their thorax and the wings vary considerably. In some of them the 3rd and 4th

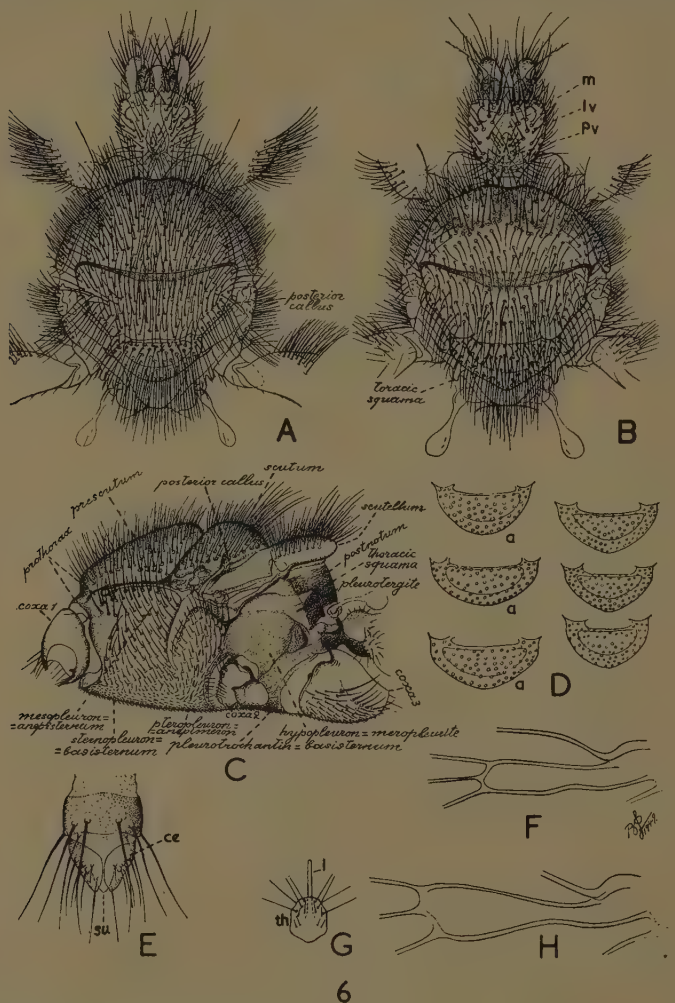


FIG. 6.—A, head and thorax of *Nycteribosca amboinensis* Rond.; B, same of *N. pretiosa* Falcoz; C, lateral view of thorax; D, forms of scutellum, and E, proctiger of *N. amboinensis*; F, first basal cell of *N. nigriceps* Jobling; G, labium, and H, first basal cell of *N. gigantea* Speiser.

longitudinal veins are strongly divergent near the wing margin, whereas in others these veins are almost parallel. These variations have also been found

in the specimens from the Philippines. Moreover, in this species the wings of the same specimen can be of slightly different forms. The only parts that do not vary much are the theca of the labium, the palpi and the proctiger. In the labium with the protracted labella the theca is always more or less conical. This condition of the theca has been found in the great majority of the specimens preserved in alcohol.

Owing to these variations it is very difficult to separate some specimens of this species from *N. pretiosa* Falcoz, of which the seven known specimens were collected in the New Hebrides, five of them on *Miniopterus australis australis* Tomas, which is also parasitized by *N. amboinensis* in the Philippines and in Australia.

It seems that in *N. amboinensis* there is a tendency to form geographical races or subspecies, but the difference between specimens from the different localities of the two geographical regions is not sufficiently clear. Apart from this, it is impossible to associate many different forms with particular species or subspecies of bats, because only about 6 per cent. of the specimens have the specific name of their mammal hosts. It is better, therefore, at present to refrain from the introduction of special names, until more material is collected and studied, especially from the Australian region and the northern and eastern parts of the Oriental region.

The previous record of this species, in the summarized form, is as follows : from *Miniopterus adversus* (Horsfield) in Amboina; from *Miniopterus schreibersi blepotis* (Temminck) in the following localities: Amboina; Myall Lakes, N.S. Wales, Australia; Tablas I., Philippines; and Adung Valley, Burma; from *Miniopterus schreibersi fuliginosus* (Hodson), in Bandoeng, Java; and in Mansacade, Ceylon; from *Miniopterus* sp. in Helvak, India; from *Pipistrellus tralatitius* (Horsfield), in Selangor, Malay Peninsular; from an unknown species of bat in the following localities: W. Java, Bolong, 600 m. alt.; and Tyibodas, Mt. Gedeh, 1400 m. alt.; Waikobocelak, Solomon Is.; Niki-Niki, Timor; Tonsville and Goode Is.; Queensland, Australia; and Nicobar Is.

Present record: 2 specimens from an unknown species of bat, Luangbay Cave (iii), Sitio Tegato, Davao City, Mindanao, P. I., 22.x.1946; 26 specimens in flight, same locality and date; 50 specimens in bag for collecting bats, same locality and date; 14 specimens from *Miniopterus schreibersi blepotis* (Temminck) and *Miniopterus australis australis* Tomas, same locality and date. As *N. amboinensis* parasitizes these species, it is more likely some of these specimens came from one bat and some from the other. Four specimens from *Rousettus amplexicaudatus* (Geoffroy) or *Eonycteris spelaea glandifer* Lawrence, same locality and date; 9 specimens from bats' dung same locality and date; 1 specimen from *Miniopterus schreibersi blepotis* (Temminck), Chillage, Queensland, Australia, 7.i.1922, coll. by C. M. Hay; 1 specimen from *Miniopterus tristis* Waterhouse, Central Cave, Cotabato City, Cotabato Prov., Mindanao, P.I., 27.xii.1946, coll. by F. Werner; 3 specimens from *Miniopterus fuscus* Bonhote = *Miniopterus schreibersi blepotis* (Temminck), Japan, Riu-Kiu Is., Okinawa Is., Ishigaki, ex collection of M. Tokuda, May, 1933; 1 specimen from *Miniopterus* sp. Paita, New Caledonia, 18.iv.1945, coll. by A. J. Nicholson; and 2 specimens from *Miniopterus macrocneme* Revilliot = *Miniopterus australis australis* Tomas, Baulopari, New Caledonia, coll. by C. L. Remington.

Nycteribosca surcoufi Falcoz, 1923.

During the redescription of this species (Jobling, 1934a), which was made from the two co-types preserved in alcohol, I could not arrange very satisfactorily the theca of the labium and the proctiger under the microscope. Therefore these parts were described as different from those of *N. amboinensis*. But in fact they have the same structure as those of the species just mentioned. *N. surcoufi* can be separated from *N. amboinensis* by the bombiform head and by the structure of the anterior part of the sternopleura. Another very slight difference is present in the scutellum, of which the broadly rounded posterior margin is slightly angular in the lateral parts and in the middle. However, it is impossible to separate this species from some specimens of *N. amboinensis*, because the form of the head, the scutellum and the sternopleura vary rather considerably in the latter species. In three specimens, which were collected from the same bat, the structure of the head was as follows: in one it was distinctly bombiform, in the second, only slightly, whereas in the third it was as in the typical *N. amboinensis*.

The species is probably a different form of *N. amboinensis*. But owing to the limited material at my disposal, I leave this question unsettled, and refer the specimen with the bombiform head to *N. surcoufi*.

The two co-types were collected in New Caledonia from an unknown species of bat.

Present record: 1 specimen together with two others which are referred here to *N. amboinensis*, from *Miniopterus macrocneme* Revilliod = *Miniopterus australis australis* Tomes, 8 miles north-west of Boulopari, New Caledonia, coll. by C. F. Remington.

Nycteribosca minuta Jobling, 1934b.

The type and the two paratypes were collected from *Hipposideros cervinus* (Gould), in the Russel Islands, Solomon Islands. It has also been recorded from *Rhinolophus megaphyllus* Gray, in the type locality, and in Cape York, Queensland, Australia.

Present record: 2 specimens from *Hipposideros cervinus* (Gould), Hollandia, Dutch New Guinea, 19.iv.1945.

Nycteribosca proxima sp. n. (fig. 7).

Close to *N. modesta*, from which it differs by the structure of the scutellum, of which the lateral parts are more broadly rounded and the posterior margin is slightly produced in the middle. Its femora much thinner and less setose, and the first longitudinal vein more strongly bent near the costal margin.

Body 1.9-2.1 mm. long in male and female respectively. Head campanulate when examined from above; mediovertex broad in the front and on each side of the postvertex; each laterovertex bears long setae; postvertex spoon-shaped, with short setae, fused with occiput, which bears two small setae behind. Eyes small, not projecting laterally. Palpi as long as broad, with broadly rounded anterior margin; their ventral surface bears a few long setae in the anterior part and much shorter ones behind. Theca of labium more or less conical, labella very small.

Thorax distinctly broader than long; its antero-lateral parts much more sloping than those of *N. modesta*; prescutum as long as scutum, with longer setae in the anterior part; scutum with longer setae in the posterior part; scutellum crescent-shaped, its lateral parts broadly rounded and the posterior margin slightly produced in the middle;

it bears many setae of varying length and four very long ones in the middle; posterior part of the thoracic squamae papilliform. Ventral surface of thorax bears many very small, uniform setae. Legs rather long; femora normal, with strong setae.

Wings 1.8-2 mm. long in male and female respectively, with rather narrowly rounded apex; 1st longitudinal vein sharply bent towards costal margin in its distal part; 3rd

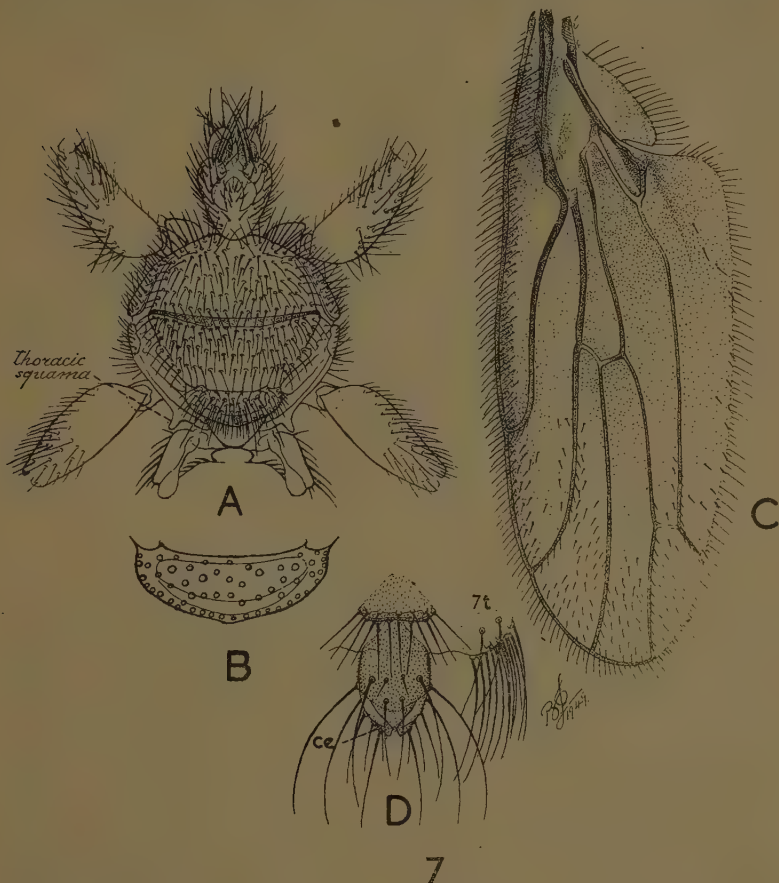


FIG. 7.—*Nycteribosca proxima* sp. n. A, head and thorax; B, scutellum; C, wing; D, proctiger; ce, cerci; 7t, seventh tergite.

and 4th longitudinal veins strongly divergent near the apex of the wing; marginal, sub-marginal and posterior cells moderately setose; alula with narrowly rounded apex.

Abdomen with many long setae on each side of its bare dorsal surface; its ventral surface bears many small setae, which in the posterior part become much stronger and longer; lateral parts of 7th tergite with many long setae. Proctiger almost cylindrical, with four dorsal, two lateral and two ventral long setae. Abdomen of male ends in a small semispherical hypopygium.

Holotype and allotype from one of the following bats: *Rousetus amplexicaudatus* (Geoffroy) or *Eonycteris spelaea glandifera* Lawrence, Luangbay Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946; 1 paratype from bag for collecting bats, and 10 paratypes collected in flight, same locality and date; 1 paratype from *Rhinolophus rufus* Eydaux and Gervais, and 21 paratypes from one of the following bats or from both: *Rhinolophus arcuatus exiguus* Andersen and *Hipposideros galeritus galeritus* Cantor, same locality and date; and 4 paratypes from bats' dung, same locality and date.

Holotype and allotype and many paratypes are preserved in the Chicago Natural History Museum. Two paratypes are in the author's collection.

Nycteribosca modesta Jobling, 1934a.

The type of this species was collected in Alutnevara, Ceylon, from *Rhinolophus rouxi* Temminck. It has also been recorded from a bat, Mao Marroe, Sumba Is., and from a bat in Camp del Monte, Philippines.

Present record: 1 specimen from *Rhinolophus virgo* Andersen, Tanabag, Puerto Princesa, Palawan I., Palawan Prov., P.I., 17.iii.1946, coll. by F. Werner; and 28 specimens from *Rhinolophus blythi blythi* Andersen, Myitkyina, Burma, 15.viii.1945, coll. by Major R. Traub.

Nycteribosca wernerii sp. n. (fig. 8).

This species resembles *N. modesta* and *N. proxima*, but is larger. It also differs from these species by its large cordiform postvertex and by the structure of the proctiger which is dome-shaped.

Body 2.4-2.7 mm. long in male and female respectively. Head cup-shaped when examined from above; mediovertex narrow; each laterovertex with a row of strong setae along the inner margin and in the lateral parts; postvertex large, cordiform, fused with occiput, with a few small setae. Eyes small, not projecting beyond the lateral margin of the head. Ventral surface of head with a row of moderately strong setae along the inner margin and weaker setae in the lateral parts. Palpi nearly as long as broad, with broadly rounded anterior margin; their ventral surface bears long setae in the anterior part and shorter ones in the posterior part. Theca of labium almost cordiform, labella very small.

Thorax distinctly broader than long; prescutum slightly longer than the scutum, uniformly setose; anterior and posterior parts of scutum with the same setae as those arising from the prescutum and with much longer setae in the middle; scutellum crescent-shaped, with short setae in the anterior and the posterior parts and six very long, thin setae in the middle; posterior part of the thoracic squamae papilliform. Ventral surface of thorax bears very small uniform setae. Legs long; femora normal, with strong setae; 5th tarsal segment large, broader than the length of all the other segments together.

Wings broad, 2.1-2.3 mm. long in male and female respectively; first longitudinal vein gently bent towards costa in its distal part; 3rd and 4th longitudinal veins divergent near the apex of the wing; anterior cross-vein distinctly longer than the proximal part of the 3rd longitudinal vein; submarginal, marginal and posterior cells moderately setose; apex of alula more or less broadly rounded.

Abdomen with a row of very long setae on each side of the bare part of its dorsal surface, and with strong but shorter setae laterally to these; its ventral surface bears many small setae; in the middle of the posterior part of this surface the setae become gradually much longer; lateral parts of the 7th tergite with a few long setae; proctiger

dome-shaped, with four dorsal, two lateral and two ventral long setae. Male abdomen ends in a semispherical hypopygium, which does not differ in its structure from that of *N. proxima*.



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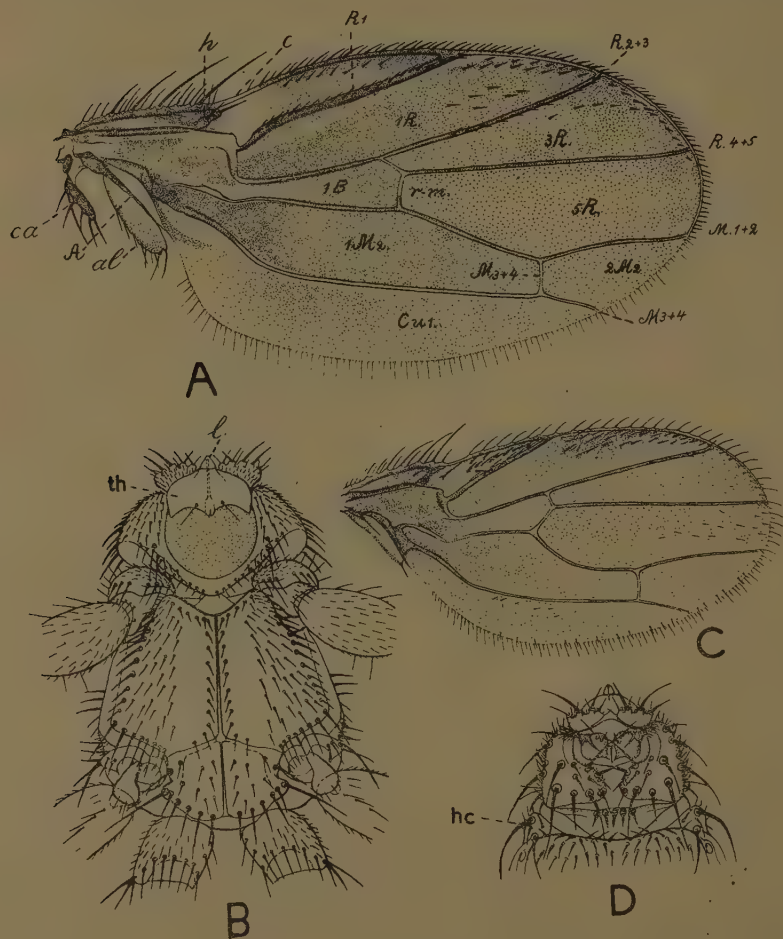
FIG. 8.—*Nycteribosca weneri* sp. n. 11, first tergite; 21, second tergite; 71, seventh tergite.

Holotype, allotype and ten paratypes were collected from *Hipposideros diadema griseus* Meyer, in Central Cave, Cotabato City, Cotabato Prov., Mindanao, P.I., 26-27.xii.1946, by F. Werner; and 1 paratype from *Eonycteris robusta* Miller, in Cave at Dilerig, Bukidnar Prov., Mindanao, P.I., collected by L. H. Phillips.

Holotype, allotype and eight paratypes are preserved in the Chicago Natural History Museum, and two paratypes in the author's collection.

Raymondia pagodarum Speiser, 1900.

During the examination of specimens of the genus *Raymondia* in the present collection, it has been found that there exists two distinct forms, both of which agree with the original description of *R. pagodarum*, but differ from each other by very distinctive characters not mentioned either by Speiser



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FIG. 9.—A, wing, and B, ventral view of head and thorax of *Raymondia lobulata* Speiser; C, wing, and D, head of *R. pagodarum* Speiser. A, anal vein; al , alula; C , costa; ca , upper calypter; h , humeral vein; hc , humeral callus; l , labella; $r.m.$, anterior cross vein; $1B$, first basal cell; M_{3+4} , fifth longitudinal vein; th , thea; R_1 , first longitudinal vein, (A, B and C from *Parasitology* (Jobling, 1930)).

(1900) or Kessel (1925). In my redescription of *R. pagodarum* (Jobling, 1930), which was made from the two imperfectly preserved specimens, these two species were also confused. Thus, drawing 5, p. 293, belongs to the undescribed species, whereas the drawing of the wing, p. 294, belongs to *R. pagodarum*. An examination of the type of *R. pagodarum*, from the Vienna Museum, showed that the head of this species is quadrangular when examined from above, its occiput has a row of short, thick setae near the dorsal margin, and the alula of its wings bears the apical seta (fig. 9 c and d). As all these characters are absent in the other form, it is described below as a new species.

The type of *R. pagodarum* was collected in Rock Temples of Seven Pagoda, in Madras, India. There is one specimen in the British Museum (Natural History), collected either from *Hipposideros larvatus* Horsfield or *Rhinolophus malayanus* Bonhote, in Biserat, Jolore, Malay Peninsula, 8.viii.1901, by R. Brown. Its records from *Hipposideros speoris speoris* (Schreiber) and *Rhinolophus affinis* Horsfield, in Ceylon, and from *Emballonura nigrescens* (Gray), in Amboina and Molucca Islands, by Muir (1912), are probably also correct. It has also been recorded from a bat in Sumba Island.

Present record: 20 specimens from *Hipposideros cervinus* (Gould), Hollandia, Dutch New Guinea, 1944 and 1945; and 1 specimen from *Rhinolophus blythi* Andersen, Burma, Myitkyina, 15.vii.1945. Collected by Major R. Traub.

***Raymondia pseudopagodarum* sp. n. (fig. 10).**

In its general appearance this species resembles very much *R. pagodarum*, from which it can be easily separated by the absence of the characters mentioned above, and by those shown in the key.

Body 1.2-1.5 mm. long (on slide) in male and female respectively. Head rounded laterally; each laterovertex with strong setae in the lateral part and with three inner setae near the posterior margin, the rest of its surface with small setae; occiput bare; ventral surface with three strong setae in front of the fore-coxa and a few small ones behind on the posterior margin. Three strong setae on each side of rostrum membrane and one in each lateral part; ventral part of genae beset with very small setae. Anterior margin of palpi with two strong setae; their ventral surface bears very minute setae. Theca of labium as long as broad in its posterior part; labella very short.

Mesonotum as long as broad; humeral calli with one very strong and several small setae; mesonotal suture complete; prescutum uniformly setose; scutum with a few small setae near the mesonotal suture and much stronger ones posteriorly to these and in the lateral parts; scutellum triangular with two strong setae far apart in the middle, and with two small setae between these and two moderately strong behind; one moderately strong seta in each lateral corner; its posterior margin bears a few small setae. Ventral surface of thorax flat, uniformly setose, except lateral and posterior margins which bear strong setae; anterior part of each sternopleuron conical, projecting under fore-coxa. Legs presenting no distinctive character.

Wings 1.3 mm. long; first longitudinal vein without setae; humeral cell with one seta; costal cell with a row or a patch of small setae and a single one close to the humeral vein; marginal cell with a few setae near the costal vein; fourth longitudinal vein strongly bent between the anterior and the posterior cross vein; alula vestigial, without apical seta.

Abdomen of female as in *R. pagodarum*, but the proctiger slightly more conical, with two dorsal and two lateral long setae. Abdomen of male resembles that of *R. pagodarum*, with large, conical hypopygium which is longer than broad.

There are two specimens of this species in the British Museum (Natural History), of which one is from an unknown host, collected in Chungking, China, February, 1913, by R. Brown; and the other is either from *Hipposideros laccatus* (Horsfield) or *Rhinolophus malayanus* Bonhote, collected by R. Brown in Biserat, Jolore, Malay Peninsula.



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FIG. 10.—*Raymondia pseudogaglionum* sp. n. (calypteron, slightly modified, from *Parasitology* (Jobling, 1930)).

Present record: 19 specimens either from *Rhinolophus arcuatus erigius* Andersen or *Hipposideros pumilus pumilus* Cantor, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946: 2 specimens from an unknown species of bat, the same locality and date: 1 specimen in cave, Malaburuan, Caburan, Davao Prov., Mindanao, P.I., 14.i.1947: 3 specimens either from *Rousettus amplexicaudatus* Geoffroy or *Emytenia spinea pinnifera* Lawrence, Luang-bay Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946: 1 specimen from *Rhinolophus cafer* Eydox and Gervais, Luang Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946: 1 specimen in flight, in cave, the same locality and date: 1 specimen from *Rhinolophus vingo* Andersen, Tanabag,

Puerto Princesa, Palawan Is., 17.iii.1947; 3 specimens either from *Miniopterus schreibersi blepotis* Temminck or *Miniopterus australis australis* Tomes, Luangbay Cave, Sitio Tegato, Davao City, Mindanao, P.I., 22.x.1946; 3 specimens from bats' dung, the same locality and date. The following specimens were collected by Major R. Traub, in Myitkyina, Burma, in 1945; 50 specimens from *Rhinolophus blythi blythi* Andersen and 3 specimens from *Hipposideros gentilis gentilis* Andersen. Holotype, allotype and many paratypes, preserved in the Chicago Natural History Museum; and 2 paratypes in the author's collection.

SUMMARY.

1. The present study of the thorax shows that the part which was previously called the metapleura consists of two sclerites: the pleurotergite and the modified thoracic squama.

The thorax of these flies, as that of the Calyptræ, has the posterior calli.

2. The abdomen of the TRICHOBIINAE and the STREBLINAE has seven pairs of abdominal spiracles. In the NYCTERIBOSCINAE the 1st pair is lost. The ASCODIPTERINAE have only three pairs, which belong to the 5th, 6th and 7th abdominal segments respectively.

As in the Calyptræ, the spiracles lie in the tergites or in the tergal part of the abdomen.

The 1st and 2nd tergites are fused together. The 1st sternite is very small, while the second sternite is very large.

In the female abdomen the tergites and sternites 4-6 and tergites 8 and 9 are absent. In NYCTERIBOSCINAE the 7th tergite is divided, the 7th sternite is fused with the 8th, and the 9th sternite is very small.

In the female abdomen of the TRICHOBIINAE and the STREBLINAE the 7th tergite is either a single small sclerite or is divided. Their 8th and 9th sternites are absent.

In all subfamilies the 10th abdominal segment forms the "anal segment" or the proctiger, which bears the cerci and the subanal plate.

The male abdomen of the NYCTERIBOSCINAE has the divided 6th tergite, while that of the TRICHOBIINAE and the STREBLINAE has the divided 5th sternite. In these two subfamilies the hypopygium consists of the synsternite and the 9th tergite. Their synsternite is formed by the fusion of the 6th, 7th and 8th sternites, and bears the 7th pair of spiracles.

The hypopygium of the NYCTERIBOSCINAE is a single arch-shaped sclerite, formed by the fusion of the 8th sternite and the 9th tergite.

The 9th tergite, except that of *Raymondia*, bears the surstili, which are homologous to the edita of *Glossina*.

In STREBLIDAE the segments forming the hypopygium undergo a process of torsion, during which the 7th and 8th segments rotate 180°, while the 9th tergite performs complete circumversion and also rotates parallel to the sagittal plane of the body.

The 9th sternite has been compared with that of *Glossina*. It is a trough-shaped sclerite, of which the anterior part is produced into the apodeme and the posterior part bears the gonapophyses.

In the higher Diptera the gonapophyses are probably derived from the processes of the 9th sternite. In STREBLIDAE they are homologous to the anterior pair of the gonapophyses of the Calyptræ.

The appendages of the 9th sternite are present only in the NYCTERIBOSCINAE, and they are regarded as homologous to the inferior claspers of *Glossina*.

The aedeagus is the tube tapering posteriorly, of which the proximal end bears the apodeme.

The morphology of the thorax and especially of the abdomen shows that the STREBLIDAE are related to the Calyptrerae.

3. The relationship of the STREBLIDAE to their hosts is influenced by the roosting habits of the bats.

The monoxenous species occur on bats which roost separately from other bats, and their distribution corresponds to that of their hosts. On the other hand, the distribution of the heteroxenous species which parasitize cave bats is much wider.

Excluding the genus *Ascodipteron*, 14 species occur exclusively in the Oriental region; 7 in the Australian region; 2 are distributed in the Oriental and the Australian regions; and 1 in the Palaearctic, the Oriental and the Australian regions.

None of the Oriental and the Australian species occur in the Ethiopian and in the Mediterranean part of the Palaearctic regions and vice versa. The distribution of the Oriental species westwards and the Mediterranean species eastwards is prevented by the winter temperature on the Iranian Plateau, where bats cannot live without hibernation.

The STREBLIDAE cannot exist on hibernating bats. Their distribution is limited by the winter isotherm of $+10^{\circ}\text{C}$., that is the temperature below which the bats begin to hibernate. In Europe they do not follow their hosts north of the January isotherm of $+10^{\circ}\text{C}$.

4. Nine species are recorded from the Philippines, and of these the following five are described for the first time: *Nycteribosca macrops* sp. n., *N. hoogstraali* sp. n., *N. proxima* sp. n., *N. werneri* sp. n., and *Raymondia pseudopagodarum* sp. n.

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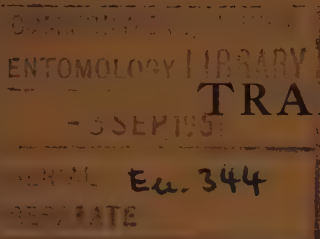
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Explanation of Reference Lettering.

A. second anal vein; *aea.* aedeagal apodeme; *ae.* aedeagus; *ago.* apodeme of gonapophyses; *al.* alula; *as.* aedeagal sheath; *C.* costal vein; *ca.* upper calypter (Calypter on); *ce.* cerci; *Cu₁*. first cubital cell; *ej.* ejaculatory duct; *gen.* genital opening; *go.* gonapophyses; *h.* humeral vein; *hc.* humeral callus; *hyp.* hypopygium; *ic.* inferior claspers; *l.* labella; *lv.* laterovertex; *M.* median veins and cells; *m.* mediovertex; *M 3 + 4.* posterior cross vein; *pr.* proctiger; *pv.* postvertex; *R.* radial veins and cells; *rec.* rectum; *r-m.* anterior cross vein; *s.* sternites; *sn.* sensory sclerites; *sp.* spiracles; *st.* surstyli; *su.* subanal plate; *t.* tergites; *th.* theca of labium; *us.* U-shaped sclerites; *1B.* first basal cell; *7 + 8s.* synsternite; *1 + 2t.* syntergite.

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THE MORPHOLOGY, TAXONOMY, AND BIOLOGY OF THE BRITISH EVANIOIDEA (HYMENOPTERA).

By R. W. CROSSKEY, B.Sc., F.R.E.S.

Manuscript received 8th September, 1950.

(Read 6th December, 1950.)

With 72 Text-figures.

GENERAL INTRODUCTION.

THE aim of the present work has been to provide a useful, accurate, and adequate account of the skeletal anatomy, the systematics, and the habit of a hitherto little known group of parasitic Hymenoptera. It is presented in two parts, which may be regarded as quite separate entities having individual introductions, illustrations, and figure-numbering. Part I commences immediately after this introduction and deals with the Morphology, i.e., the external and internal cuticular structure, of the Evanioidea, while Part II is concerned with their taxonomy and biology. This procedure it is felt is justified, for although an understanding of taxonomy must be based upon some general knowledge of morphology, the latter may be treated quite independently of systematics. The Evanioidea are a small group of Hymenoptera which have unfortunately suffered from neglect, most workers on the Order having been necessarily pre-occupied with the study of the larger or more economically important forms such as the ICHNEUMONIDAE. The position which they occupy in the Hymenoptera has been discussed later in the introduction to the morphology section; in the latter care has been taken not to express any particular view of the fate or homology of a suture or sclerite too dogmatically, for dogmatism on insoluble points is a failing to which too many morphologists are apparently prone.

In Part II, Taxonomy, there arises the age-old bone of contention as to whether taxonomists should adopt a strictly morphological nomenclature. The difficulty in so doing is exemplified by the cumbersome symbols that would be employed for instance to denote a single cell of the wing. Therefore in many cases names so well established in the literature as "abdomen" for gaster and "mesonotum" for mesoprescutum plus mesoscutum have been retained in the present work. Such absurdities as metathorax for propodeum have, however, been abandoned.

Finally, with regard to the biology of the British Evanioidea, there is such extreme paucity of available information that rather than create a third disproportionately small section it has been considered better to incorporate what is known in the descriptions of the individual species.

PART I.—THE MORPHOLOGY OF THE BRITISH EVANIOIDEA.

With 41 Text-figures.

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1. INTRODUCTION.

The Evanioidea form a small super-family of parasitic Clistogastran Hymenoptera; they therefore possess those characters diagnostic of the Order such as two pairs of membranous wings and the retention of mandibles, features which place them among the sub-order Clistogastra such as the presence of a propodeum, and thirdly the nature of the ovipositor, the "two-jointed trochanter," and solitary habit, which are characteristic of the Parasitica. Before considering the morphology of the Evanioidea it will be as well here to give a brief résumé of the chequered classificatory history that the group has had, in order to show that greater awareness of morphological differences must lead to the

recognition that the insects concerned have little relation with the Ichneumon-oidea.

There are four genera occurring in Britain, viz., *Aulacus*, *Evania*, *Brachygaster*, and *Gasteruption*, all of which in the time-honoured taxonomic works of Schletterer and Kieffer were included in a single family, the EVANIIDAE. Later the EVANIIDAE, together with the ICHNEUMONIDAE, BRACONIDAE, and the small family STEPHANIDAE, were grouped to form the super-family Ichneumonoidea; it was recognized, however, that the differences within the EVANIIDAE were such as to necessitate its division into sub-families, and some recent classifications therefore include *Aulacus* in the AULACINAE, *Brachygaster* and *Evania* in the EVANINAE, and *Gasteruption* in the GASTERUPTIONINAE. In the present work the three sub-families are raised to family status, i.e., the AULACIDAE, EVANIIDAE, and GASTERUPTIONIDAE, for the differences are so great that they preclude the possibility of there being any close phylogenetic relationship. It is the contention of the writer that these three families should be removed from the Ichneumonoidea and raised to super-family rank as the Evanioidea. This group, it must be freely admitted, is mainly one of convenience for a collection of probably ancient, and certainly widely divergent forms, which cannot be "fitted" elsewhere. They do, though, possess many common characteristics which, while relating them among themselves, also clearly separate them from the Ichneumonoidea; the two most important are the presence of a costal cell in the fore wing and the dorsal insertion of the gaster on the propodeum. It is also the very different formation of the wing venation and gaster in the three constituent families of Evanioidea which makes it impossible to suppose that there is any close relationship within the super-family. These points are brought out more fully later in the descriptions of the morphological structures concerned.

The following account of the morphology of the Evanioidea is particularly that of the genus *Gasteruption* with additional notes on the other three genera. The latter have been treated more fully where there are wide differences, as in wing-venation, the form of the gaster, and the male genitalia.

Examinations of specimens have all been carried out on pinned material, from the collection of Dr. O. W. Richards, either without treatment or after partial desclerotization by immersion for 24 hours in cold caustic potash (10 per cent. soln.). In order not to damage whole specimens the male genitalia were quite easily extracted after relaxation without potash treatment; they, together with such structures as the mouthparts, were transferred to and cleared in cedar-wood oil, if necessary after dehydration in alcohol. Almost all the illustrations have been made with the aid of a squared-eyepiece; those of the wings alone, however, were drawn from canada-balsam mounts using a camera lucida.

2. THE INTEGUMENT, SCULPTURE AND CLOTHING.

The integument is for the most part heavily sclerotized, membrane being restricted chiefly to those regions requiring flexibility of movement. The most extensive membranous area occurs on the ventral side of the prothorax, but membrane is also present in the oral fossa, suspending the mouthparts from the head-capsule, in the cervical region between head and propleuron, and as the intersegmental membrane of the abdomen.

The head and thorax are variously sculptured, though the gaster is smooth. The sculpture may vary from fine shagreenation of the surface to coarse wrinkling and reticulation, together with close or diffuse puncturation. Usually strong sculpturing is particularly evident on the notal region of the mesothorax, and on the propodeum.

Both head and thorax bear a varying amount of silvery pubescence, although the eyes are almost without exception glabrous. Macrotrichia or setae, commonly known simply as hairs, occur on the legs and palpi and maxillary lobes, while on the paraglossal sclerites these form stout bristles.

3. THE HEAD.

The following account of the morphology of the head, while approximately representing the Evanioidea as a whole, relates to the GASTERUPTIONIDAE in particular; the AULACIDAE and EVANIIDAE differ mainly in the complete absence of cephalic sutures, the great development of the malar area, and the short and broad occipital region.

(a) *The Head-capsule.*

The shape of the head-capsule is as shown in fig. 1. The long axis is vertical, i.e., the head is orthognathous (hypognathous), in which respect it may be regarded as primitive, recalling the condition in the Orthoptera; laterally it bears large elliptical compound eyes. On the dorsum of the head, between the compound eyes, are three ocelli, disposed in a triangle, and with the median ocellus anterior. Postero-ventrally the head-capsule is hollowed out to form the *oral fossa* (fig 2), contained in which are the freely movable mouthparts suspended from the cranium by extensive membranes. Posteriorly the relatively small *foramen magnum* is situated in the centre of a deep depression which is bounded peripherally by an *occipital carina*, the nature of which is of specific importance, being sometimes represented as a wide reflexed collar, and sometimes almost absent. The posterior region of the head, between the foramen magnum and the oral fossa, forms a bridge the nature of which is considered below. An abbreviated membranous cervical region connects the head with the propleura of the thorax, the lateral walls being strengthened by a pair of *cervical processes of the proepisterna* (fig. 10).

Sutures of the head-capsule.—The sutures delimiting the cephalic sclerites have become largely obliterated, although their positions may possibly be represented by carinae, as occur for instance in the hypostomal region. At this point it may be remarked that whereas an internal ridge is often upheld as evidence of the position of a suture, great reluctance is often shown in accepting a carina as such conclusive proof. There seems little reason for supposing, however, that should a flange arise at the suture formed by the edges of adjacent sclerites it could not equally easily be an external carina as an internal ridge. It is therefore simplest, and in the absence of any evidence to the contrary, justified to regard the occipital and hypostomal carinae as representing the positions of the occipital and hypostomal sutures respectively.

The antero-dorsal region of the head bears an almost imperceptible line, sometimes impressed, and sometimes raised, which has been doubtfully held to represent the *coronal suture* (fig. 1). The ventral end of the latter bifurcates

into two sutures which extend ventro-laterally towards the antennal sockets. These sutures (fig. 1) have been homologized with the *frontal sutures*, but if the median ocellus, as is commonly held, is borne on the frons, the so-called coronal suture must represent the two confluent frontal sutures, which redivide forming an arm running towards the antenna of each side. If this supposition of the fate of the frontal sutures is correct, the frons must be restricted to a region immediately below the bifurcation, and to an area of indefinite size surrounding the median ocellus. Further, it must be borne in mind that the so-called coronal suture may be in fact purely superficial, and possess no homology with any suture of the primitive Pterygote head; support for this

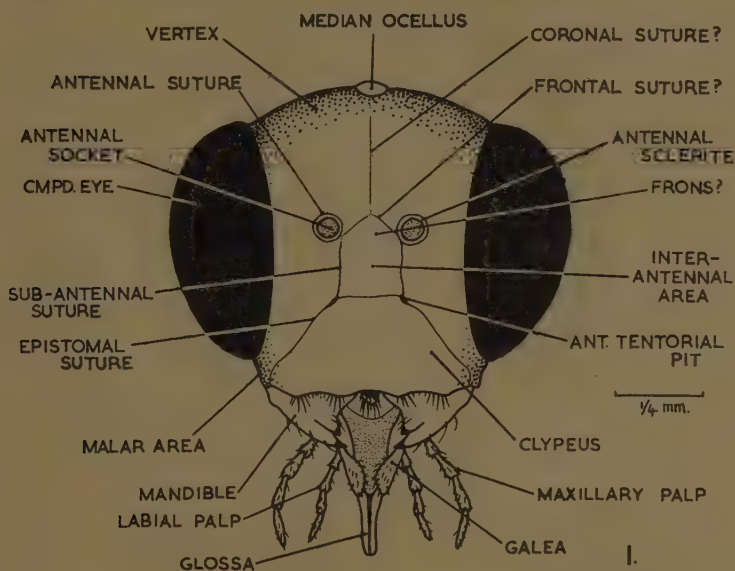


FIG. 1.—*Gasteruption jaculator*. Anterior view of head.

view is afforded by the fact that no trace of any such suture occurs posteriorly to the median ocellus.

Extending downwards from the inner edges of the antennal sockets are a pair of sutures which appear in some individuals to be continuous with the ventral ends of the diverging frontal sutures (?), and which themselves end ventrally in the anterior tentorial pits; these may be referred to as the *sub-antennal sutures* (fig. 1), a name which avoids the necessity of employing a strictly morphological term for structures of unknown homology. The well-marked anterior tentorial pits serve to fix the identity of the *epistomal sutures* (fig. 1), which run from them ventro-laterally to the margin of the head so as to cut off the cranial condyles for mandibular articulation from the clypeus; the tentorial pits are connected transversely by a suture, which is probably the continuation of the epistomal sutures, in which case the epistomal suture as a

whole delimits a sub-triangular sclerite, the clypeus. It is possible, though, that the sub-antennal sutures and so-called frontal sutures are the actual continuation of the epistomal suture, and that the transverse suture between the anterior tentorial pits is a later development, which would then separate an ante-clypeus from a post-clypeus.

On the lateral and posterior aspects of the head there is no indication of a pleurostomal suture, which makes it impossible to define accurately the

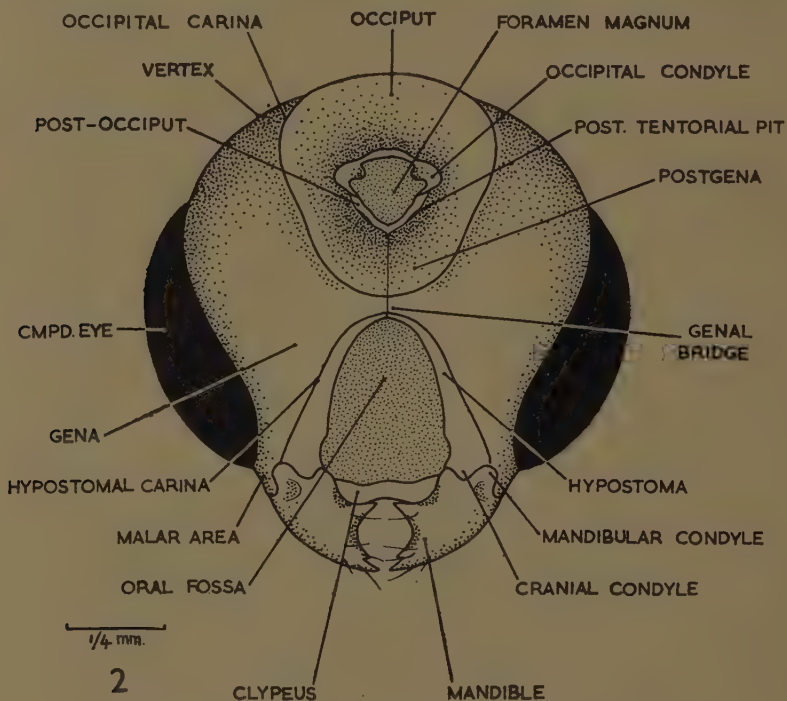


FIG. 2.—*G. jaculator*. Posterior aspect of head, with mouthparts removed.

limits of the malar area and gena. A *hypostomal carina* (fig. 2), probably marking the course of the hypostomal suture, extends round the oral fossa, ending at the cranial acetabula for mandibular articulation. A median definitive suture transverses the bridge between oral fossa and foramen magnum, forking just before reaching the latter, and forming the *post-occipital suture*, which, after crossing the posterior tentorial pits, continues round the foramen to separate a ring-like post-occiput from the occiput and post-gena. An *occipital carina* (fig. 2) probably represents the position of the occipital suture.

In addition to the foregoing sutures there are immediately surrounding each compound eye an ocular suture, and at the base of each antenna, separating the antennal sclerite from the cranium proper, an *antennal suture* (fig. 1).

Sclerites and areas of the head-capsule.—Owing to the obliteration or partial absence of the bounding sutures the extent of the cranial sclerites can only be gauged very approximately, and it is therefore preferable to speak of the cephalic areas rather than sclerites as indicative of this uncertainty of limitation.

The *clypeus* is a flat plate forming the antero-ventral region of the head, from the anterior tentorial pits to the mandibles; both dorsally and laterally it is bounded by the epistomal suture, but there may, as has already been discussed, be an ante- and a post-clypeus. The latter would then correspond to the region here called the *inter-antennal area* (fig. 1), which lies between the sub-antennal sutures, and the former to the region here called the clypeus (fig. 1). The greatest difficulty of homologizing the areas of the head is provided by the *frons*, the fate of which is capable of at least four different expositions. In the first place it may have become eliminated completely by the migration and fusion of the frontal sutures in the midline, and the so-called frontal sutures being in fact the epistomal suture; in this case the inter-antennal area would be a post-clypeus. Secondly the frons may have become partially obliterated by the fusion of the proximal ends only of the frontal sutures, when it would remain as the area around the median ocellus, and as the inter-antennal area either in whole or in part. The third possibility is that the median suture is quite superficial, being no part of the original epicranial suture, in which case the frons might occupy a considerable area of the face quite incapable of any definite limitation. Lastly, while it has always been assumed that the median ocellus must be borne on the frons, there is no real reason for supposing that it cannot be borne on the vertex; if this was so the so-called coronal suture could in fact be the stem of the primitive Y-shaped epicranial suture, and the bifurcating arms the actual frontal sutures, the whole complex then resembling that of a more generalized insect, with the sole exception that the median ocellus would lie in the course of the coronal suture, instead of in the angle formed by the frontal sutures. The frons would then be that area lying between the frontal sutures and the clypeus, i.e., the region here named the inter-antennal area.

The parietal regions of the head consist of the *vertex*, which bears the paired posterior ocelli and extends back to the occipital carina and laterally on each side to the genae; each *gena* (fig. 2) meets its fellow of the opposite side in the *genal bridge* (fig. 2). Immediately posterior to the genae, but separated therefrom by the ventral part of the occipital carina, are the *postgenae* (fig. 2). The latter similarly meet each other in the mid-line as a postgenal bridge, which forms by far the greatest part of that region of the cranium lying between the oral fossa and the foramen magnum. Dorsal to the latter but lying within the occipital carina is the *occiput* (fig. 2); both this region and the postgenae are separated from the foramen magnum by a narrow annular sclerite, the *post-occiput* (fig. 2), which is limited externally by the post-occipital suture. Above the foramen the post-occiput forms a narrow curved strip, but at the dorso-lateral angles it is enlarged to form two rounded eminences, the *occipital condyles* (fig. 2). The major part of the cranium is therefore formed of two "segments," an anterior parietal segment formed of dorsal vertex and lateral genae, and a posterior occipital segment of dorsal occiput and ventral postgenae, the two segments being entirely separated by the occipital carina. This view of the extent of the morphological areas, it must be pointed out, is based upon the

aforementioned assumption that the occipital carina arises at the position of the occipital suture.

The part of the head capsule below and in front of the gena is the *malar area* (figs. 1 and 2); this lies between the eye and the mandible of each side, and provides a condyle on which the latter can rock; it corresponds to the region frequently referred to as the "cheek" in taxonomic literature. The hypostomal region consists of two elongate *hypostomata* (fig. 2), which together completely surround the oral fossa, and meet dorsally to form a very narrow hypostomal bridge. The outer edges of the hypostomata are formed by the hypostomal carinae.

The labrum and epipharynx, while morphologically parts of the head proper, are described later in relation with the mouthparts.

Apart from the sclerites and cranial areas already described, there remain for mention the ocular ridge, which is a circular chitinous flange invaginated along the course of each ocular suture, and the *antennal sclerites* (fig. 1). The latter are small rings of chitin cut off from the cranium by the antennal sutures. Each receives the bulb of the scape of the antenna, and provides a socket in which antenna can rotate.

The tentorium (figs. 3 and 4).—The tentorium or cephalic endoskeleton is well developed; it is formed by invagination from the surface of the head, the points from which invagination has taken place remaining as well-marked tentorial pits. The *anterior tentorial pits* lie in the epistomal suture, at the dorso-lateral angles of the clypeus, while the *posterior tentorial pits* are situated in the post-occipital suture immediately below the foramen magnum. The posterior pits are connected transversely by a stout, arched, *tentorial bridge*, which gives off dorsally, and in the median line, a forwardly directed, slightly curved tentorial spine. Each end of the tentorial bridge just before the posterior tentorial pits, is connected with a thin, cylindrical, horizontal arm which crosses the cavity of the head, to reach the anterior tentorial pit of its respective side. These chitinous rods are the *anterior tentorial arms*, each of which gives off a *dorsal tentorial arm*, directed towards the antennal socket. The point at which a dorsal arm terminates beneath the surface of the cranium varies within a species. In most individuals it does so immediately under the centre of the antennal socket, sometimes beneath the edge of the latter, and occasionally near the ocular margin. When not under the antennal sockets the positions of the ends of the dorsal tentorial arms are marked on the surface of the head by slight depressions or dorsal tentorial maculae. The part of the anterior tentorial arm between the base of the dorsal arm and the anterior tentorial pit is slightly downwardly curved, and is produced internally into a flange; immediately posterior to the anterior pit the flange is continued round from the inner side to the ventral side of the arm.

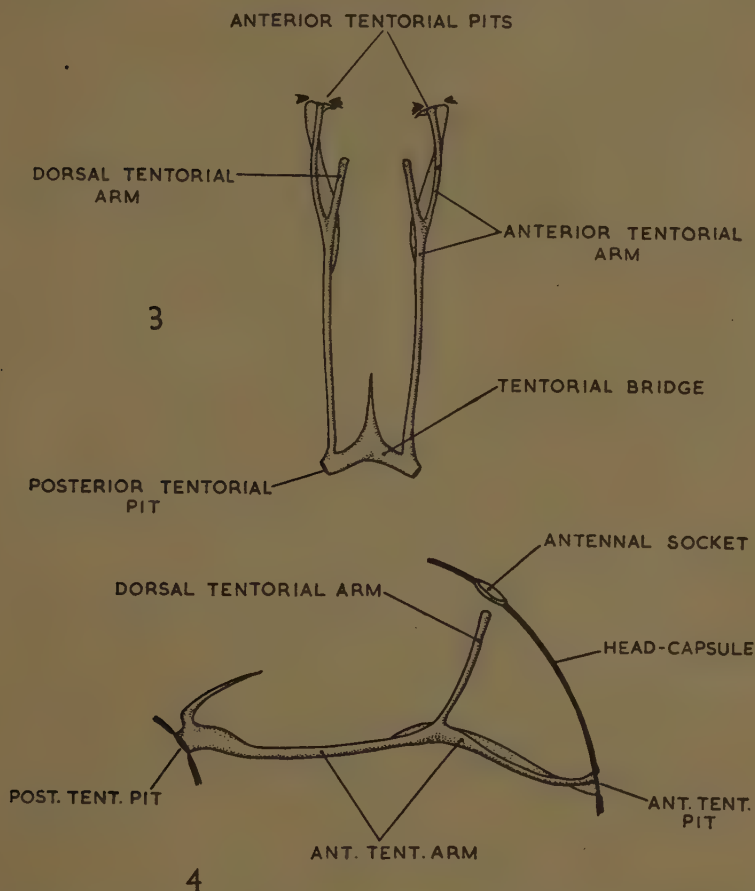
Not only does the tentorium function for general bracing and strengthening of the head but it also serves for the insertion of certain muscles operating the antennae and the mouthparts.

(b) *The Head Appendages.*

The head appendages are the antennae and the mouthparts.

i. *The antennae*.—The antennae of the Evanioidea are of the filiform type and exhibit none of the differentiation which occurs in other parasitic Hymenoptera such as the Chalcidoidea. They are 14-segmented in the male and 13

in the female. The first segment or *scape* is thicker than the succeeding segments, and articulates by a ball-and-socket joint with the antennal socket of the cranium. The second segment, the *pedicel*, is the smallest segment of the



FIGS. 3, 4.—*G. jaculator*. (3) Dorsal view of tentorium removed from head-capsule. (4) Right lateral view of tentorium with outline of head-capsule in section.

antenna, and is succeeded by the undifferentiated *flagellum* of 11 or 12 similar segments.

ii. *The mouthparts*.—The mouthparts comprise the mandibles and what may be termed the labio-maxillary complex. The mandibles function more as tools than as masticatory organs and are consequently remote from the mouth opening, feeding being carried out by the maxillae and labium. The latter are

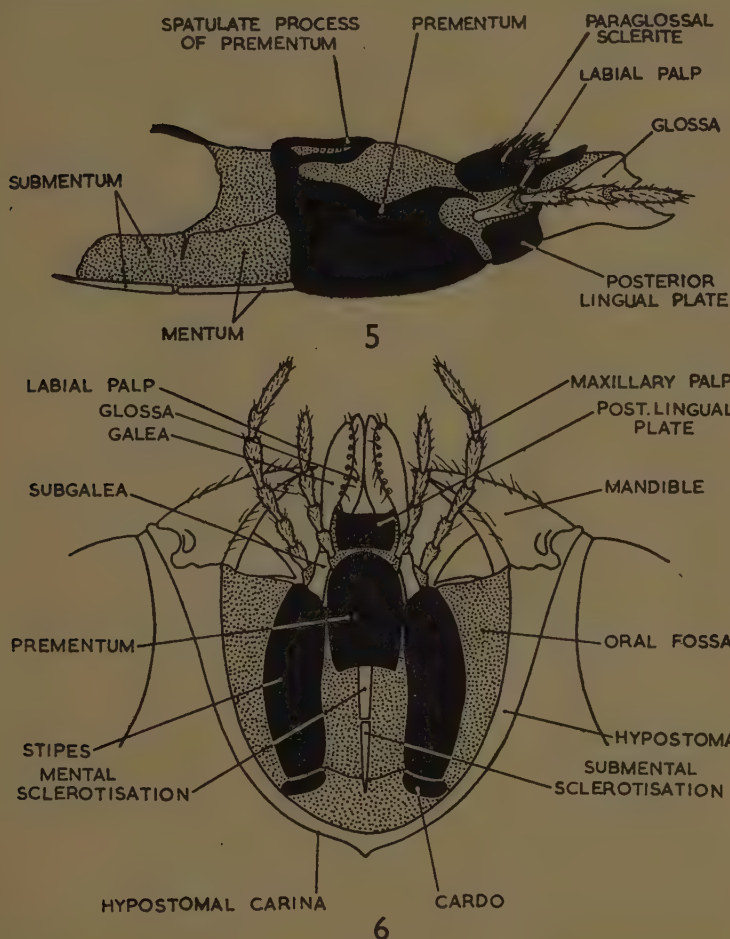
united by extensive membranes into a labio-maxillary complex, which is itself freely suspended by other membranes from the oral fossa of the cranium. The whole membranous system has been named the oral field (Duncan) or the mouth-field-sack (Mundfeldsack) of Ulrich. It serves for the contemporaneous extension of the maxillae and labium.

(1) *The mandibles* (fig. 9).—The mandibles work in the normal horizontal manner, and when at rest are folded across one another behind the clypeus. The cutting edge of each has three teeth (two in *Evania*), two terminal, and one at right angles to the mandibular axis. Each mandible is operated by two muscles; the *abductor muscle* is inserted on to the mandible near the posterior articulation or the mandibular condyle, while the *adductor muscle* is inserted by the anterior articulation or mandibular acetabulum. Two articulations enable a mandible to rock against the cranium; the anterior one is formed of a cranial condyle on the malar area, immediately posterior to the clypeus, and a *mandibular acetabulum* or ginglymus, and the posterior one of cranial acetabulum at the ventral end of the hypostomal carina and a *mandibular condyle*. A second, smaller cranial condyle occurs on the hindmargin of the head at the distal end of the hypostoma, and occupies a small hollow in the base of the mandible.

(2) *The labio-maxillary complex*.—The labio-maxillary complex comprises those organs most intimately associated with mastication and feeding, viz. the two maxillae and the labium.

The maxillae: In the resting state the maxillae occupy a position on either side of the labium, around which the maxillary lobes are adpressed distally, and are attached by membrane to the edge of the oral fossa (fig. 6). Each maxilla (fig. 7) is well sclerotized, except for the lacinia, which is fairly fleshy. The *cardo* is a small, almost rectangular sclerite, closely applied to the base of the stripes, with which it forms a movable hinge. When at rest the cardines are orientated almost horizontally, but when the mouthparts are extended they assume an almost verticle position. The stipes is elongate, and is sclerotized in two parts which are united by a narrow strip of membrane; the basistipes, here referred to simply as the *stipes*, is the larger of the two, and when looked at from the posterior aspect (fig. 6) is rectangular, but from the inner lateral aspect (fig. 7) is pointed distally. The second, more distal sclerite of the stipes may be called the *subgalea*, and from the posterior aspect is only visible apically. It is elongate in form, and provided with an inner median projection for the articulation of the lacinia, and a distal projection for articulation of the galea. Externally it supports the base of the *maxillary palp* which in all Evanioidea is 6-segmented. The palps are moderately long, and have the distal end of each segment only lightly sclerotized. The two maxillary lobes are well developed. The *galea*, like the lacinia, is flattened and foliaceous and only weakly sclerotized; its flat surfaces bear a number of hairs, which on the inner edge are arranged as a marginal fringe of stout comb-like setae which may be termed a *galeal pecten*. The base of the galea articulates externally with the subgalea, and internally with the *basal sclerite of the lacinia*, a curved sclerotized bar also supporting the lacinia. This basal sclerite is produced apically into a small outwardly-directed tooth which meets a similar inwardly-directed tooth at the distal end of the subgalea, immediately adjacent to the base of the galea. The *lacinia* is fleshy and foliaceous, and has a marginal row of small bristles. It is supported by a small, heavily

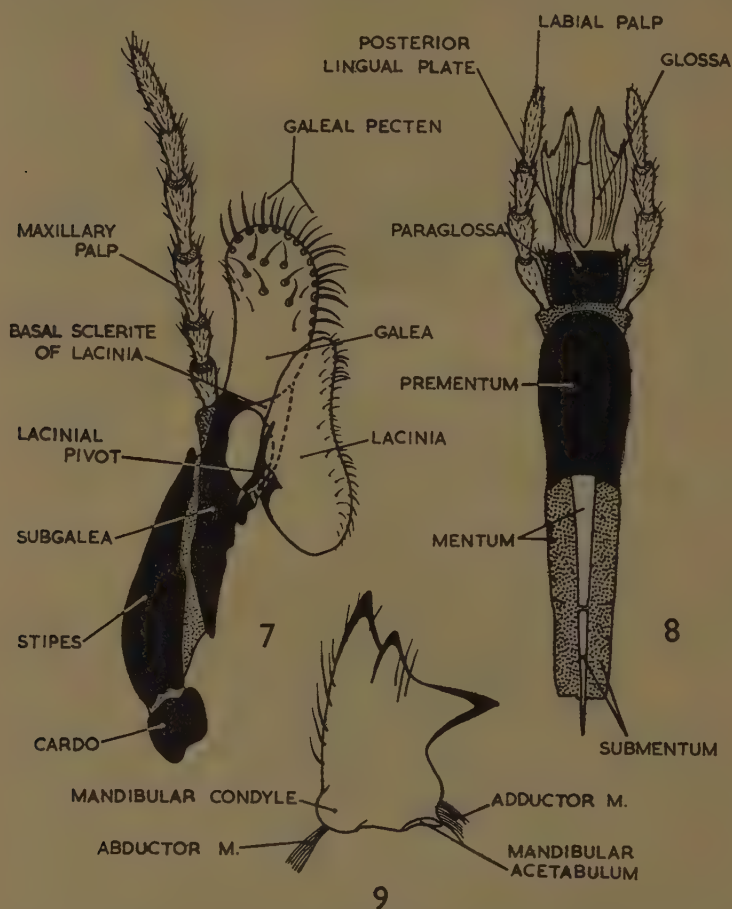
sclerotized, *lacinial pivot* which has two points of articulation, one with the basal sclerite of the lacinia, and the second with the subgalea. This second articulation is by means of a backwardly-directed process which rocks in a



FIGS. 5, 6.—*Gasteruption*. (5) Right lateral view of labium. (6) Mouthparts *in situ* from the posterior aspect.

hollow on the inwardly-directed median projection of the subgalea. The apical half of the latter and the basal sclerite of the lacinia together enclose an almost circular cavity in the maxilla. Normally the laciniae are adpressed against the sides of the labium, and the galeae are folded round the ligula with the galeal pecten directed posteriorly.

The *labium* (figs. 5 and 8): As the head is orthognathous the labium is normally more or less vertical in position, but in the following description the terms dorsal and ventral are substituted for anterior and posterior respec-



FIGS. 7-9.—*Gasteruption*. (7) Postero-lateral view of inner side of left maxilla. (8) Posterior view of labium. (9) Posterior aspect of right mandible.

tively, in virtue of the fact that usually the labium is removed from the head for examination.

The principal sclerite of the labium, as established by Snodgrass for the Hymenoptera generally, is the *prementum*. This is a large, strongly convex, boat-shaped plate on the ventral surface, which is produced antero-laterally into two curved processes which surround the bases of the labial palps. Postero-

laterally the prementum is produced into two processes which reach the dorsal side, and bend forwards again to form the *spatulate processes of the prementum*. These are connected by membrane in the mid-line, while membrane also extends from each to the inner sides of the stipites. In contrast to this well-developed prementum the postmental region is very poorly developed, being largely membranous, except for two small sclerotizations on the ventral surface. The distal one of these is elongate and rectangular, and lies immediately posterior to the prementum; it may be called the *mental sclerotization*. The proximal *submental sclerotization* is small and dagger-shaped and lies behind the mental sclerotization. The mentum and submentum are separated by a weakening in the membrane, and by a distinct suture between the sclerites. Also on the ventral surface of the labium and visible when the head is viewed from beneath is a quadrate sclerite separated from the distal end of the prementum by a very narrow band of membrane. This sclerite is the *posterior lingual plate* which covers the base of the lingua; it is produced distally into two processes, which extend laterally round the labium just anterior to the points of insertion of the palpi almost to meet two similar processes developed on the paraglossal sclerites. The terminal labial structures are similar to those of other parasitic Hymenoptera, the glossae being well-developed, and the paraglossae reduced. The glossae are fused to form a fleshy lingua, often spoken of simply as the *glossa*; that this structure is of twofold origin is evident, as there is a dorsal line of union from which extend two pointed lateral lobes. The latter are adpressed to one another ventrally, and are normally closely enveloped by the galeae. The *paraglossae* are reduced to two small strongly sclerotized *paraglossal sclerites*, each of which bears distally a tuft of stout chaetae, and which lie on either side of the lingua, near the bases of the labial palps. Each sclerite is produced into a forwardly directed process, and a small process which lies laterally and approaches a similar process of the posterior lingual plate. The dorsal surface of the labium between the spatulate processes and the lateral edges of the prementum and between the paraglossal sclerites is entirely membranous. The *labial palpi* are 4-segmented as in all Evanioidea; they are inserted laterally on the labium on a small membranous projection just distal to the prementum. Each segment is elongate and only lightly sclerotized apically.

(3) *The labrum and epipharynx*.—In many insects the labrum and epipharynx are developed so as to participate in feeding, although they are morphologically parts of the head-capsule. Although this is not the case in Evanioidea, or in fact in any Hymenoptera, these structures are described as is customary, in relation with the mouthparts.

The *labrum* (fig. 23) is small and concealed behind the clypeus. It consists of a lightly sclerotized transverse bar, which is produced abruptly into a median ventral well-sclerotized and narrow process. The latter bears a terminal tuft, and the bar a marginal row, of bristles. Basally the labrum is attached to the inner side of the clypeus by a broad band of membrane, which presumably represents the clypeo-labral suture and an unsclerotized area of the labrum. The *epipharynx* (fig. 23) is a membranous flap arising at the base of the labrum, and lying behind the latter. It is almost triangular in form but with two faintly-marked rounded lobes laterally, and with the apex immediately posterior to the median process of the labrum.

4. THE THORAX.

(a) *The Thoracic Trunk.*

As in all higher Hymenoptera, the first abdominal segment is fused with the thorax, and the region of the body thus constituted should therefore be referred to as the thoracic trunk or alitrunk. The first abdominal segment is usually held to be represented only by the tergite of the segment, which is spoken of as the propodeum or median segment. Owing to the intimate relationship between propodeum and thorax the two will be described together as the thoracic trunk. In the Evanioidea there is no well-marked line of union between propodeum and metathorax, although this is usually indicated by an alteration in the nature of the sculpturing, and by a shallow depression. The form of the thoracic trunk in *Aulacus* and *Gasteruption* is somewhat elongate, but in *Evania* and *Brachygaster* it is more or less quadrate when viewed from the side. The whole structure is very rigid, strongly sclerotized and sculptured and bears the wings and the legs. Membrane is restricted to the procoxal articulations, the ventral surface of the prothorax, and to very narrow strips along certain sutures which allow a very small amount of flexibility. Cavities also exist in the dorso-lateral walls of the thorax for the insertion of the wings. There has been considerable fusion of adjacent thoracic areas, so that the mesopleura and mesosternum have been united into a single sclerite, as have the metapleura, metasternum and propodeum, thus increasing the rigidity of the thorax.

The endoskeleton of the thorax is very well developed; in each segment i.e., the prothorax, mesothorax, and metathorax, there are similar cuticular invaginations, differing only in proportion from one another. For convenience, therefore, only that of the mesothorax will be described in the following account. The internal skeleton serves for muscle attachment and additional strengthening of the thorax, while the thoracic cavity is largely filled by the muscles which operate the wings.

The prothorax.—The prothorax has lost all semblance of a typical segment, and forms a suspensorium for the anterior pair of legs. The *pronotum* (figs. 10 and 13) is entirely roofed over by the greatly developed mesonotum. It consists of two lateral subtriangular or quadrate sides connected anteriorly by a narrow, transverse, collar-like band. Posteriorly each side is developed as a *posterior pronotal lobe* (fig. 10), which overlies the first thoracic spiracle, and which has a slight hollow concavity which accommodates the *tegula*. In *Gasteruption* each front angle of the pronotum is produced as a short blunt *pronotal process*. Dorsally and posteriorly distinct sutures separate the pronotum from the mesonotum and the mesopleuron respectively, while ventrally it is attached by membrane to the propleura and the first coxae. The *propleura* are short, and orientated almost vertically in the EVANIIDAE, but in GASTERUPTIONIDAE and AULACIDAE are produced longitudinally to form an elongate structure, the so-called "neck" of taxonomists. Each propleuron is strongly convex laterally, bears a fine carina, and meets its fellow of the opposite side in both a dorsal and a ventral line of union (figs. 11 and 12). These propleura are commonly held, in the Hymenoptera, to be the *pro-episterna*, the proepimeral elements being either very reduced or altogether absent. According to Snodgrass traces of an epimeron are present in certain Aculeates. The

cephalic end of a propleuron is produced into a small dagger-shaped *cervical process of the pro-episternum* (fig. 10). The latter is possibly a ventral cervical sclerite which has become united with the prothorax, as no definitive cervical sclerites exist in the short membranous cervicum. Although the processes may be pleural in nature Crampton holds that a large part of the sclerites here called pro-episterna are of cervical origin and has therefore proposed the term cervico-propleuron. Posteriorly the propleura diverge slightly to allow of the insertion of the anterior part of the *prosternum* (fig. 11). This is a small though very evident sclerite lying on the ventral surface of the prothorax immediately posterior to the propleura and between the front coxae. It shows superficially

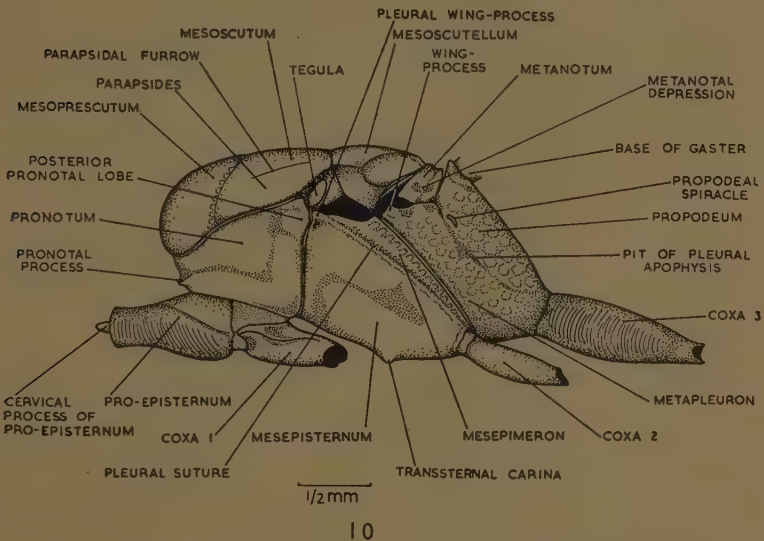
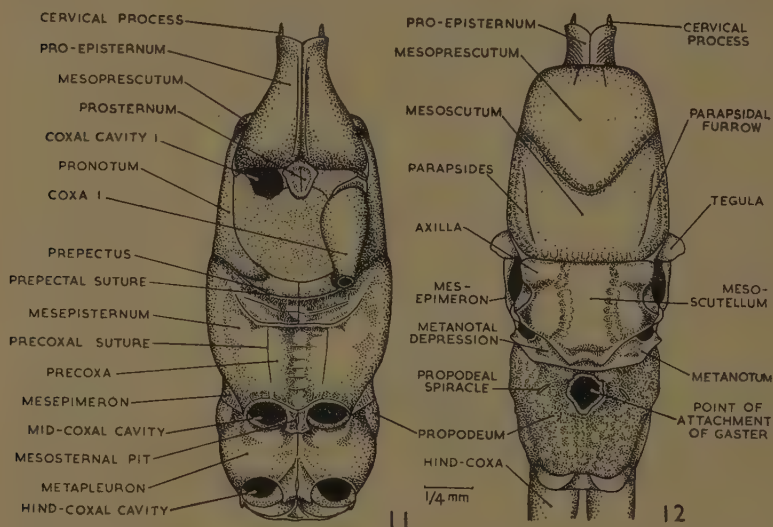


Fig. 10.—Left lateral view of thoracic trunk of *Gasteruption*.

a fine longitudinal line along which the prothoracic endoskeleton is invaginated. The latter is a complex structure differing only in point of proportion from that in the mesothorax.

The mesothorax.—The mesothorax is the largest segment of the alitrunk, and bears the anterior pair of wings and the middle pair of legs. It has departed from the primitive appearance of a segment in that the notal region has been largely shifted forwards to occupy an excavation in the dorsum of the preceding segment. The mesonotum (fig. 12) is differentiated into the *mesoprescutum*, *mesoscutum*, and *mesoscutellum*. The prescutum is strongly curved, and anteriorly it bears two very shallow diverging grooves, the so-called notal sutures: posteriorly it is limited from the scutum by a curved transverse groove in *Gasteruption* and by paired longitudinal grooves (particularly deep in *Evania* and *Aulacus*) in the other Evanioidea. In AULACIDAE and EVANIIDAE the prescutum therefore extends back as far as the scutellum and divides the scutum

into two lateral parts. Each part of the divided scutum, or each side of the single scutum of *Gasteruption*, bears a longitudinal impressed line, the *parapsidal furrows*. The latter cut off the *parapsides* to the outside. The anterior notal wing-processes, which are normally borne on each parapsis in the Hymenoptera, are apparently not developed. Lying immediately behind the scutum, and separated therefrom by the transscutal suture, is the scutellum. The definitive scutellum comprises the primitive scutellum of generalized insects and the anterior *axillae* (fig. 12) which are stated in the Hymenoptera to be derived from the scutum. The actual scuto-scutellar suture therefore coincides with the transscutal suture, which separates the true scutum from the true scutellum,

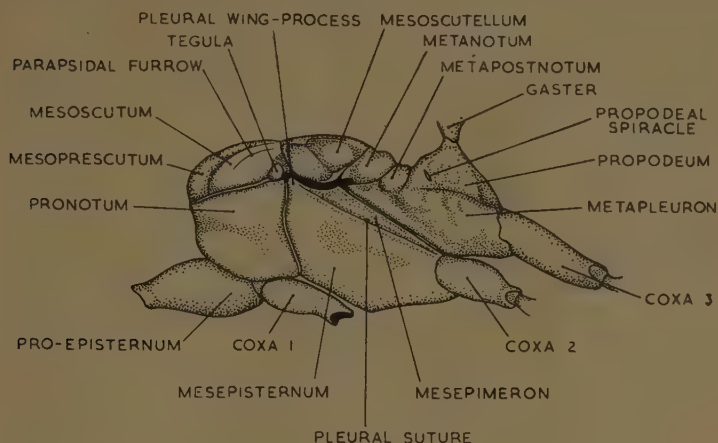


FIGS. 11, 12.—*Gasteruption*, thoracic trunk. (11) Ventral view. (12) Dorsal view.

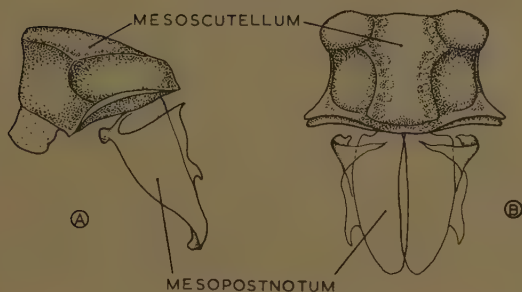
only in the middle part of its length. Axillae are not apparent in *Brachygaster*. Posterior to the axillae the scutellum consists of a raised central region and lateral scutellar pockets. In EVANIIDAE the former is very wide and the latter small. The hind margin of the scutellum forms a flange in *Aulacus* and *Gasteruption* which bounds the lateral scutellar pockets and overlies the front of the metanotum medially. In *Gasteruption* the antero-lateral scutellar corners are developed as two flat processes within the thorax, (fig. 14, A). The *mesopostnotum* (fig. 14) is represented by an extensive phragma (mesopostphragma) of a bipartite nature attached dorsally to the posterior edge of the scutellum and occupying a transverse position within the thoracic cavity, between the mesothorax and the metathorax.

The lateral walls of the mesothorax are formed by the mesopleural element lying between the pronotum and the metapleura. The mesopleura are not separately sclerotized, but are continued ventrally by a region of very doubtful homology. This whole sclerite may be termed the mesopectus. The greater

part of each side of the mesopectus is formed by the *mesepisternum* (fig. 10), the *mesepimeron* being reduced to a narrow posterior strip. Dorsally the epimeron reaches forwards to the pronotum, adjacent to which it forms a knob, the *pleural wing-process* of the forewing. The *pleural suture* (figs. 10 and 13)



13



14

Figs. 13, 14.—(13) Left lateral view of thoracic trunk of *Aulacus striatus*. (14) The mesopostnotum of *Gasteruption*, (A) left lateral, (B) dorsal.

between episternum and epimeron is marked in the Evanioidea, as in most other Hymenoptera, only by a superficial change of contour and sometimes of sculpture. The anterior part of the mesothorax is differentiated ventrally as a band-like subsclerite, the *prepectus* (fig. 11) or epinemium, formed of episternal and sternal elements, and apparently peculiar to the Hymenoptera. The prepectus lies between the downwardly directed sides of the pronotum, and

bounds the ventral membranous area of the prothorax. It is limited behind by the epinemial carina which arises at the position of the *prepectal suture*. The ventral surface of the mesothorax is also crossed by two other carinae behind the prepectus, the anterior of which is certainly, and the posterior probably, purely secondary. This posterior ridge, or trans-sternal carina of Duncan, may possibly, however, represent in part the anterior ends of the precoxal sutures. Between this carina and the mid-coxal cavities are two poorly marked longitudinal grooves which have received various interpretations. They are found in most other Hymenoptera, and according to Duncan are quite superficial developments in the VESPINÆ; they have also been held to be the pleurosternal sutures, i.e., the lateral limits of the mesosternum, in which case the latter would be a large and distinct sclerite. Recently the view has been gaining acceptance that the furrows are the *precoxal sutures* (fig. 11), which run from the outer edges of the coxal cavities, round the rims of the latter, and then forwards towards the prothorax. If this supposition is correct the region between the grooves is the precoxal bridge, with the mesosternum either occupying a narrow strip in the mid-line and not demarcated laterally, or else entirely invaginated within the thoracic cavity. Posteriorly each *precoxa* is produced backwards to form a tooth between the mid-coxal cavities. The postcoxa if present at all is suppressed to a narrow band behind the coxal cavity.

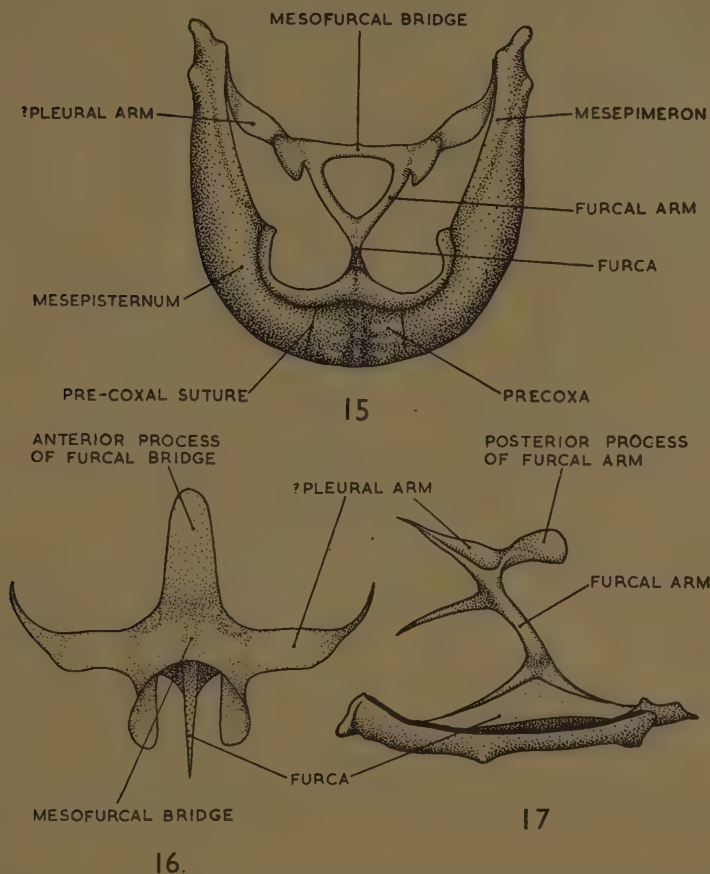
The internal skeleton of the mesothorax is very well developed, and possibly wholly arises by invagination from the sternal region. As previously mentioned, it is possible that the mesosternum is quite unrepresented externally and that the median ventral surface is formed by the precoxæ which are pleural in origin. Whatever the superficial nature of the sternum there arises internally in the mid-line a longitudinal invagination, the mesosternal apophysis or *furca*. The dorsal margin of this median ridge is thickened and produced in the middle of its length into a pair of diverging *furcal arms* (figs. 15 and 17), which are connected with one another dorsally by means of a *mesofurcal bridge* (figs. 15 and 16). The bridge is produced anteriorly into the median *anterior process of the furcal bridge* (fig. 16), while each furcal arm bears dorsally a backwardly directed *posterior process of the furcal arm* (fig. 17). Each end of the furcal bridge is produced into a curved dorsally directed arm which is closely applied to the inside of the upper end of the pleural suture. These arms may be developments from the ventral furcal element of the endoskeleton, or they may be *pleural arms* (?) (fig. 15) formed by invagination from the pleural sutures which have become fused with the furcal arms and have only retained a weak connection with the pleuron. If they have originated from the sternal apophysis there is no pleural apophysis. Duncan maintains that this is the case in *Vesputa*.

The foregoing account of the endoskeleton of the mesothorax is also generally applicable to the prothorax and the metathorax.

The boundary between the mesothoracic and the metathoracic segments is marked by a well-developed suture between the mesepimeron and the metapleuron of each side, which continues round ventrally just behind the mid-coxal cavities and above the mesosternal teeth.

The metathorax.—The pleural and sternal regions of the metathorax are completely fused with the propodeum to form a single sclerite. The *metanotum* (fig. 12) is a transverse sclerite lying behind the scutellum, which is frequently

spoken of erroneously in taxonomic works as the postscutellum. In *Gasteruption* the metanotum is very narrow, so that the point of attachment of the gaster is approximated to the scutellum (fig. 12), but in EVANIIDAE and *Aulacus* it is broader and the gaster is remote from the scutellum (fig. 13). The sides of



FIGS. 15-17.—*Gasteruption*. (15) Posterior aspect of the mesothoracic endoskeleton and mesopectus. (16) Dorsal view of the mesothoracic endoskeleton removed from the mesopectus. (17) Left lateral view of mesothoracic endoskeleton, with mesopleura removed.

the metanotum are hollowed out to form two fossae, the *metanotal depressions*. Feebly developed notal wing-processes enable the hind wings to articulate with the metanotum. The *metapostnotum* in GASTERUPTIONIDAE and EVANIIDAE is not distinguishable, being intimately incorporated into the propodeum, but in *Aulacus* (fig. 13) it is found as a definite sclerite which is marked off from the

propodeum behind by a transverse suture, and from the metapleuron below by a short curved groove.

The metapleura and metasternum are united as a complete sclerotization which, although not separated from the propodeum, may be separately described as the metapectus. The *metapleuron* (figs. 10 and 13) is smaller and simpler than the mesopleuron and exhibits no trace of any differentiation into episternum and epimeron. Antero-dorsally each metapleuron has a small protuberance, the pleural wing-process of the hind wing. The metapleura lie ventral or antero-ventral to the propodeum. The difficulty in interpreting the ventral region of the mesothorax is similarly encountered in the metathorax. The limits of the metasternum are undiscernible, but there is a median sternal groove which opens behind into a metasternal pit similar to the *mesosternal pit* (fig. 11). Between the metacoxal cavities the sternum is produced backwards as a pair of metasternal teeth. From the metasternal pit and groove an elaborate endoskeleton is invaginated, similar to that in the mesothorax, but differing in that there is also a *pit of the pleural apophysis* (fig. 10) in the metapleuron. The hind coxae are closely articulated to the metapleura.

The propodeum.—It is now firmly established that the propodeum or median segment is derived during development from the first abdominal segment, and that it is in fact the first tergite of the abdomen. In many Hymenoptera it is an independent sclerite separated from the preceding metathorax by a good suture, but in Evanioidea there is no such distinction, the line of union only being indicated by a shallow furrow, or by a change in sculpture, with no additional internal evidence. The propodeum in *Gasteruption*, *Brachygaster* and *Evania* is a strongly sloping curved plate providing the posterior declivity of the thoracic trunk, but in *Aulacus* it is pyramidal in form and is situated dorsal to the metapleura. The most characteristic feature of the propodeum is that the gaster is inserted at its most dorsal point, instead of as in almost all other Hymenoptera between the hind coxae. This single point precludes there being any relationship, or certainly very little, between the Evanioidea and the ICHNEUMONIDAE. In fact this feature of the abdomen provides the strongest reason for removing the GASTERUPTIONIDAE, EVANIIDAE and AULACIDAE from the super-family Ichneumonoidea, and elevating these three families to super-family rank as the Evanioidea.

Dorso-laterally the propodeum has a pair of slit-like *propodeal spiracles* (figs. 10, 12 and 13), sometimes placed on low eminences. Immediately above the bases of the posterior coxae the propodeum projects as a pair of flanges, the apical scales of the propodeum.

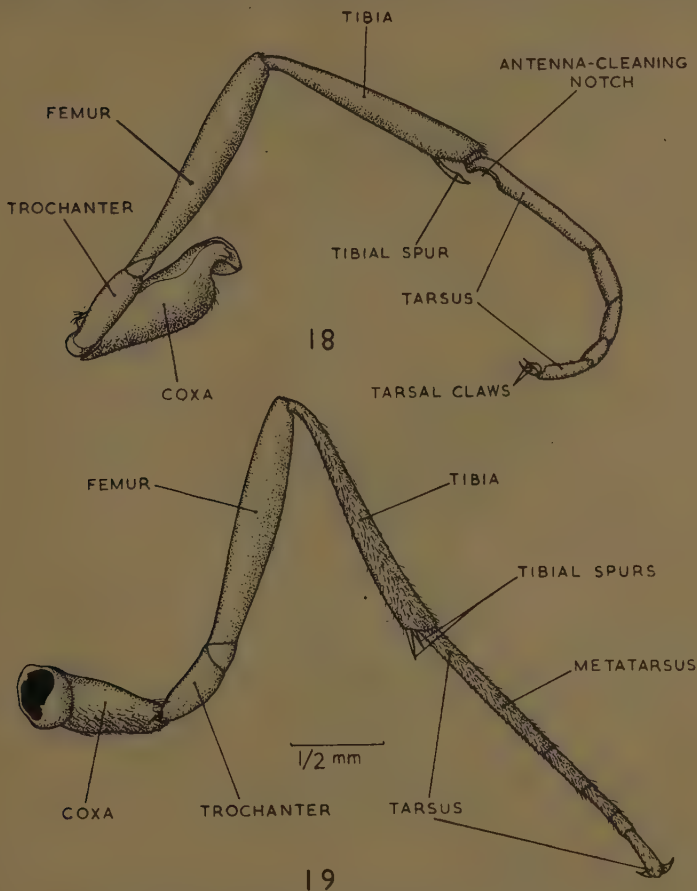
(b) *The Thoracic Appendages.*

The thoracic appendages are the legs and wings.

i. *The legs.*—The legs of the Evanioidea call for comparatively little mention. They are unspecialized and possess the normal five segments, the last of which is further subdivided into five tarsomeres, the basic number in the Insecta. The anterior legs are the shortest and the posterior the longest, being particularly long in *Evania*. The front legs each have the characteristic antenna-cleaning device of the Hymenoptera.

The *coxae* (figs. 13, 18, and 19) are cylindrical in most, but conical in *Brachy-*

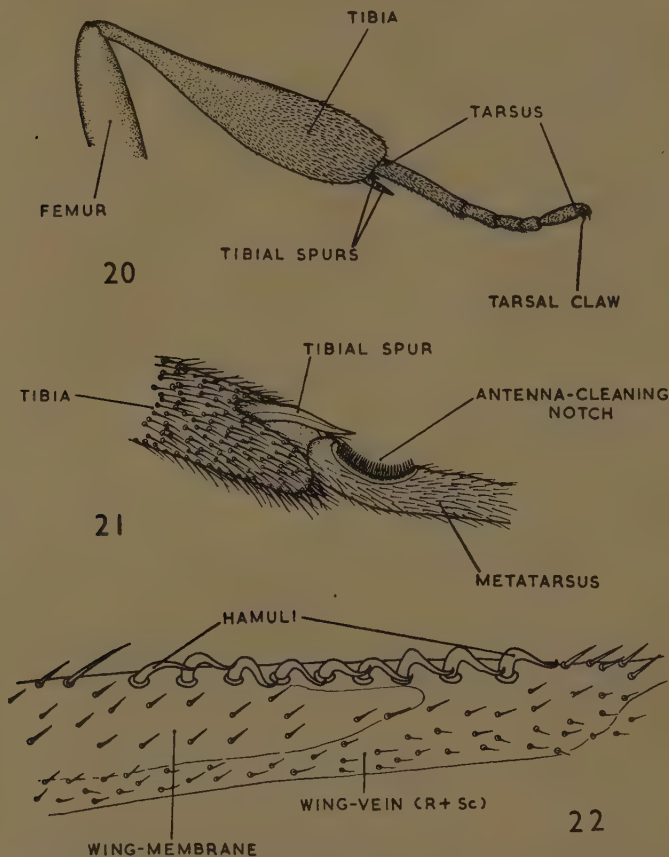
gaster. The middle and hind coxae are very rigidly attached to the thorax, but the front ones are only loosely suspended from the prothorax so as to allow great mobility of the fore legs for antenna-cleaning purposes. The front coxa has a process which articulates with a similar process on the propleuron. The



FIGS. 18, 19.—*Gasteruption*. (18) Fore leg. (19) Mid leg.

trochanters (fig. 18) are small, and closely united with the *femora*. The latter are cylindrical and unmodified, except that each femur has a small piece differentiated basally, which is referred to in taxonomy as a second division of the trochanter. This "two-jointed trochanter" is a feature of all *Parasitica* except the *Cynipoidea* and the *PELECINIDAE*. The *tibiae* are subcylindrical, except for the hind tibiae of *Gasteruption*, which are strongly clavate (fig. 20). The middle and hind tibiae each have two *tibial spurs* terminally, and each

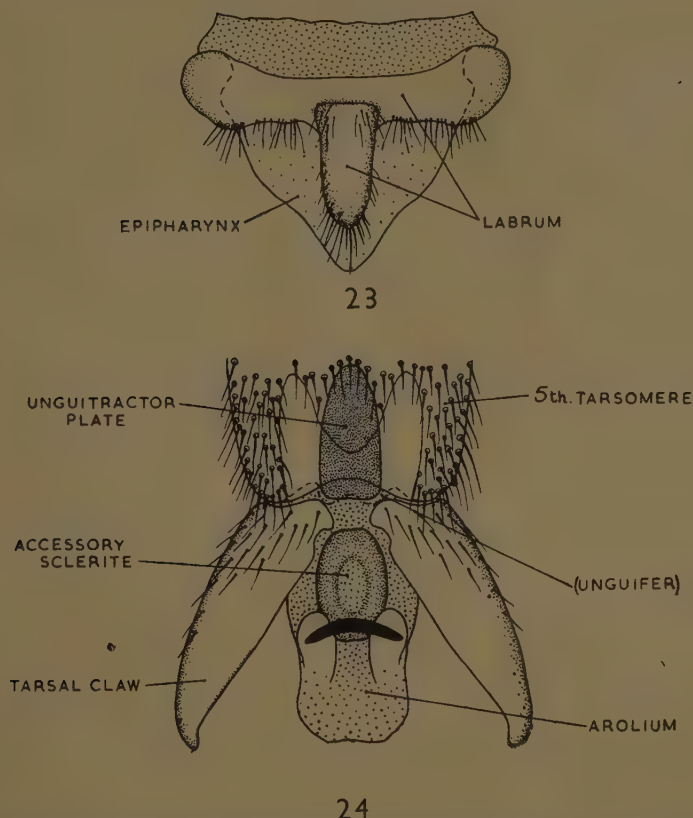
front tibia one modified spur arising from a membranous pocket (fig. 21). The *tarsi* are elongate, and each is divided into five subsegments or tarsomeres. The first tarsomere or *metatarsus* is always longer than any of the succeeding ones, and in the hind tarsus is as long as the four other tarsomeres together.



FIGS. 20-22.—(20) Part of hind leg of *Gasteruption* to show the clavate tibia. (21) Portion of fore leg of *Gasteruption* greatly enlarged to show the antenna-cleaning device or strigil. (22) Costal margin of the hind wing of *Evania* showing the hamuli for locking the fore and hind wings together; greatly magnified.

The last tarsal joint bears a number of terminal structures collectively termed the pretarsus which have been examined in *Gasteruption* (fig. 24). The dorsal end of the fifth tarsomere is slightly produced into a bilobed projection, the *unguifer* (shown in transparency by a broken line in the illustration). To the unguifer are articulated the lateral tarsal claws or ungues. Between the ungues is a large blunt soft pad, the *arolium*, which is as long as each unguis, and is

variously sclerotized ventrally. Occupying a median position on the arolium is an oval *accessory sclerite*, distal to which is a pair of light sclerotizations; overlying the latter and the end of the accessory sclerite is a very heavily sclerotized horseshoe-shaped bar extending round the arolium. Situated in a cavity in the end of the last tarsal segment is the *unguitractor plate*.



FIGS. 23, 24.—*Gasteruption*. (23) Labrum and epipharynx in anterior view. (24) Structure of pretarsus; ventral. The unguifer on the dorsal side is shown by a broken line and the name appears in brackets.

The antenna-cleaning device or strigil (fig. 21) is formed at the junction of the front tibia and tarsus. It comprises a curved tibial spur with a distinct "edge" acting as a scraper, and a notch in the proximal end of the metatarsus. The notch itself is long and shallow, but is lined with a row of about 25 stout pegs. The tibial spur projects from a terminal hollow in the tibia and works against the metatarsal excavation, so that any foreign matter collected on the antenna

is removed by drawing that structure through the cavity between spur and notch.

ii. *The wings*.—As in all Hymenoptera, there are two pairs of membranous wings articulated to the dorsal side of the thorax, the fore pair being larger than the hind. The fore wing and hind wing of each side are locked together by means of a number of chitinous hooks or *hamuli* (fig. 22), which engage with the recurved posterior margin of the fore wing or frenal fold. The hooks are borne on the lightly sclerotized costal margin of the hind wing. The number of hamuli is constant within the genus; thus in *Aulacus* there are two, in *Brachygaster* four, in *Evania* (fig. 22) a row of ten (the first rather weak), and in *Gasteruption* three. In the last-named genus the second and third hooks are separated from the first by a greater distance than that between each other. The wing-membrane is hyaline and strong, but is covered with very short hairs (fig. 22); each wing also has a marginal row of fine hairs. At a point on the anterior margin of the fore wing the wing-membrane is thickened and chitinized, forming the pterostigma (Ps) which is strictly a cell.

The articulation of the wings: The wings are inserted on to the thorax between the notum and the pleuron of both the mesothoracic and the metathoracic segments. The notal wing-processes are hardly represented at all, but there are well developed pleural wing-processes. At the base of each wing and serving to articulate it with the thorax are the axillary sclerites, while there are also some additional sclerotizations which overlie the bases of the more anterior veins. There are three axillary sclerites; the fourth axillary of some Hymenoptera appears not to be developed. The *first axillary* of the fore wing lies against the parapsis of the mesonotum, and of the hind wing articulates to a slight projection of the metanotum; its anterior neck articulates with the subcostal sclerite. The *second axillary sclerite* is articulated below to the pleural wing-process of the epimeron, is articulated on its inner side to a projection on the first axillary, and articulates by its outer end to the *third axillary sclerite*. The latter is the outermost of the three, and is associated with the broadened base of the anal vein. Traversing the slight thoracic hollow in which the base of the wing is set is the very distinct flexor muscle of the wing, which is inserted on to a posterior process of the third axillary. The additional sclerites of the wing-base are associated with the proximal ends of the wing-veins. Lying in the middle of the wing-base is the single sausage-shaped *median plate*. Normally in insects this sclerite is associated with the bases of the media and cubitus, but in Evanioidea the Cu and M form a common vein which is fused proximally with the radius and subcosta (R + Sc). A number of small pteralia overlie the bases of the costa and the common base of the radius and subcosta; on the costal margin is an elongate *humeral plate* which is articulated to the proximal end of the costa. Between the humeral plate and the wall of the thorax is interpolated a small *costal sclerite* which underlies distally an anterior projection on the *subcostal sclerite*. The latter is a large plate overlying the base of the subcosta, and having three projections on the inner side which articulate with other pteralia; the anterior projection is mentioned above; the middle projection articulates with a hollow in the anterior end of the first axillary, and the posterior process articulates with a small protuberance on the anterior end of the second axillary.

The venation of the wings: The nomenclature of the wing veins and cells has

probably provided more difficulty, and been the subject of more varying interpretations, than any other point in the morphology of Hymenoptera or even the insects as a whole. The first good system was that proposed in the early nineteenth century by Jurine and which has remained in use by taxonomists to the present day; its best recommendation is its simplicity and the ease with which it may be applied to all Hymenoptera, but its defect lies in that it makes no attempt at homology with the veins of other insects. Modifications of the Jurinian system were later made by Rohwer, Gahan, Cresson and others, but it was not until the work of Comstock and Needham that the subject was placed on a firm morphological basis. Their system was made by apparent homologizing with other orders, but it seems unnecessarily complicated, as also does its more recent modification by Bradley. The nomenclature proposed by Tillyard was simpler, but based on fossils believed by him to be ancestral to the Hymenoptera, a belief which has since been proved erroneous. Ross (1936) has put forward a quite different nomenclature founded on the assumption that the Hymenoptera had a Panorpid ancestry which is gaining gradual recognition; his system is adopted here, as it is probably the most accurate and certainly the most convenient. Unfortunately the exact homologies will probably never be known, as in Hymenoptera the formation of the wing veins precedes the outgrowth of the tracheae.

The most primitive wing-venation in Evanioidea is shown by *Aulacus*, but the venation of the other genera may be attributed to reduction from this form. A table is given below of the nomenclature of the veins and cells of *Aulacus* according to Comstock and Needham, Tillyard, and Bradley, the systems being related to the old Jurinian names and the new scheme proposed by Ross. Diagrams of this basic venation of the Evanioidea are given which show the variations of interpretation of the above authors.

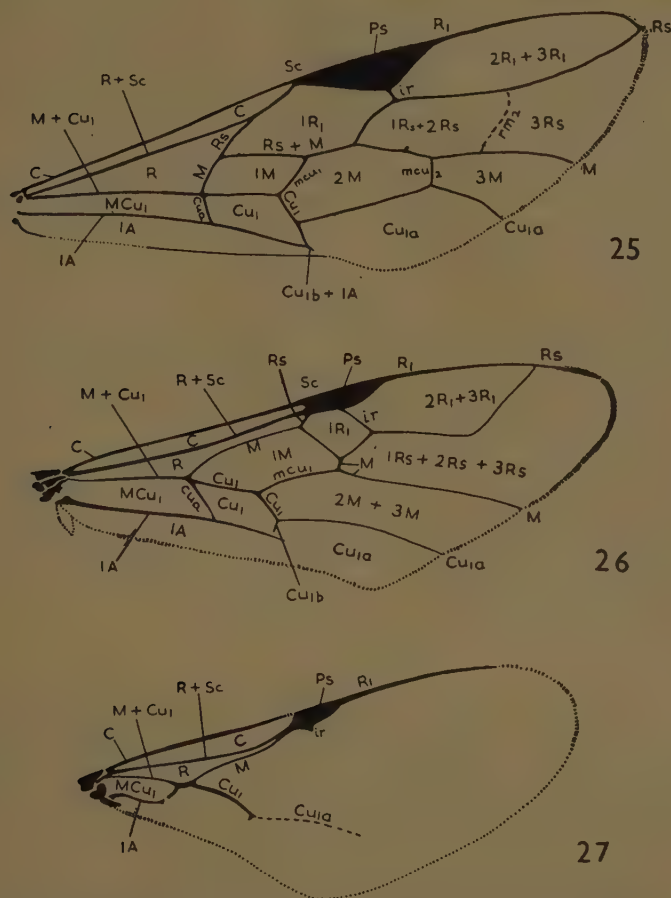
The Variations in the Venation of Evanioidea (Nomenclature of Ross):

The venation of the fore wings is well developed in all except *Brachygaster*, but in the hind wings the veins are almost obsolete, or perhaps their courses are represented by differences of level of the wing surface. Faint sclerotizations in the hind wing are sometimes present which are the costa and the Sc + R. In the fore wing of all Evanioidea there is a costal cell, in which feature the group differs from all other Clistogastran Hymenoptera except for the small family STEPHANIDAE. The venation is quite different from that in the ICHNEUMONIDAE and BRACONIDAE, and provides some justification for removing the ancient families AULACIDAE, EVANIDAE and GASTERUPTIONIDAE from the Ichneumonoidea and raising them to a super-family. In fact the resemblances to the ichneumons are purely superficial, and if any relation with these exists it is very distant, as is evidenced by the widely different nature of the attachment of the petiole for instance. On the basis of the venation alone the Evanioidea cannot be regarded as a very homogeneous group for although the veins of *Evania* and *Gasteruption* can be homologized with those of *Aulacus* there are extraordinary differences of proportion, and it is in fact possible that some cells do not correspond with those they appear to. The fore wing of *Evania* (fig. 26) differs from *Aulacus* (fig. 25) as follows: Rs does not reach the wing apex so that cell $2R_1 + 3R_1$ is shorter and broader; cell 1M is greatly enlarged so that $1R_1$ is reduced; both rm_1 and rm_2 are absent so that $1Rs$, $2Rs$

Nomenclature of the Wing Veins and Cells in Evaniaidea.

Jurinian and modifications.	Comstock and Needham.	Tillyard.	Bradley.	Ross.
1. Long Veins :				
Costa . . .	C	C	C+Sc	C
Subcosta . .	Sc+R+M	Sc+R+M	Sc+R+M	So+R
Radial vein .	r+R ₃₊₄ +R ₅	rm+M ₁₊₂	ir+Rs	ir+Rs
Cubitus . .	M+M ₁₊₂ +R ₅ + R ₄ +M ₁	M+M ₃₊₄	M+M ₁₊₂	Rs+M+M
Discoidal vein	M ₄ +M ₃	Cu ₁ +icu	Cu ₁ +Cu ₁ +M ₃₊₄	Cu ₁ +Cu _{1b}
Subdiscoidal vein	m+M ₂	Cu ₁	M ₃₊₄	Cu _{1a}
Cubital vein .	Cu+Cu ₁	Cu	Cu+1A	M+Cu ₁
Anal vein . .	1A+2A+3A+ M ₃₊₄ +Cu ₁₊₂	1A+Cu ₂ +1A	2A+Cu ₂ +2A	1A+Cu _{1b} +1A
2. Cross-veins :				
Basal vein . .	M+mcu	M+mcu ₁	M+mcu	Rs+M
Nervulus . .	M ₄ +Cu ₁	Cu ₂	Cu ₂	cua
1st transverse-cubital vein	rm+R	M ₁₊₂	rm ₁ +Rs	Rs
2nd transverse-cubital vein	R ₅	im ₁	rm ₂	rm ₁
3rd transverse-cubital vein	R ₄	im ₂	rm ₃	rm ₂
1st recurrent vein	M ₃₊₄	mcu ₂	M ₃₊₄	mcu ₁
2nd recurrent vein	M ₂	mcu ₃	im	mcu ₂
3. Cells :				
Costal	C	C	C+Sc+Sc	C
Subcostal or median	M	bm	2M	R
Median or submedian	Cu+Cu ₁	bca	1M+Cu+1A	MCu ₁
Anal . . .	3A	a	2A+3A	1A
Radial or marginal	2R ₁ +R ₂	3r	2R ₁ +R ₃	2R ₁ +3R ₁
1st cubital or 1st sub-marginal	R+1R ₁	r	R+1R ₁	1R ₁
2nd cubital or 2nd sub-marginal	R ₅	2m	1Rs	1Rs
3rd cubital or 3rd sub-marginal	R ₄	3m	2Rs	2Rs
4th cubital or 4th sub-marginal	R ₃	4m	3Rs	3Rs
1st discoidal .	M ₄	1sm	1M ₄	1M
2nd discoidal .	M ₃	2cu	Cu ₁	Cu _{1b}
3rd discoidal .	1M ₂	2sm	1M ₂	2M
1st posterior or 2nd posterior or 1st apical	M ₁	3sm	2M ₂	3M
	2M ₂	3cu	2M ₄	Cu _{1a}

and 3Rs, are confluent; mcu_2 is absent so that 2M and 3M are confluent; cell R is greatly narrowed, and MCu_1 is shortened. It should be pointed out that in the British species of *Aulacus*, viz., *A. striatus*, only the posterior stump of



FIGS. 25-27.—(25) Venation of fore wing of *Aulacus striatus* on the nomenclature of Ross. The venation almost approximates to that of the hypothetical form, except for the almost complete loss of the crossvein rm_1 and the partial loss of rm_2 . (26) Venation of the fore wing of *Evania appendigaster* according to Ross. (27) Fore wing of *Brachygaster minutus* named on Ross's system.

rm_1 remains, and rm_2 is weak. In *Gasteruption* Rs reaches the wing apex; rm_1 and rm_2 are absent, as also is mcu_2 , so that as in *Evania* 1Rs, 2Rs and 3Rs are confluent, as are 2M and 3M. The cell 1M is very reduced, narrow and rectangular, so that instead of M + Cu_1 branching to form a piece M meeting the

reflected Rs, this piece is absent; consequently the vein $R_s + M$ in the middle of the wing appears to spring from the end of the cell MCu_1 and not from the cell R as in *Aulacus*. The cell $1R_1$ is enlarged owing to the reduction of $1M$ and cell Cu_1 has assumed a curious shape because of a deflection of $1A$. In *Brachygaster* very little venation remains, though such as there is shows a marked similarity to that of *Evania*. The cell R is narrowed as in that genus; Cu_1 remains and there is a trace of Cu_{1a} . The vein ir is represented by a stump. *Gasteruption* therefore appears to be the form least conformable to the basic plan, particularly as the basal vein of systematists instead of being $M + R_s$ as in the others is formed of R_s only (fig. 28). To summarize these differences it may be said that basally greatest similarity exists in *Aulacus* and *Gasteruption*, while apically *Gasteruption* is like *Evania*; *Brachygaster* (fig. 27) basally resembles *Evania*, while the widest differences among all Evanioidea occur in the middle region of the wing.

It will be useful finally to summarize Ross's interpretation of Hymenopteran wing-venation as it applies to the Evanioidea:

The subcosta is fused with the radius.

The radius has two branches, the anterior branch or R_1 forming the posterior boundary of the darkened cell or pterostigma (present in all Evanioidea) and continuing as the front margin of the wing beyond the stigma, and the posterior branch which is reflected at one point being the R_s .

The media is unbranched (a difference from all other systems), and basally is fused with the Cu_1 ; in the middle of its length it is fused with R_s but distally is free to the wing-margin.

The cubitus is confluent basally with the media and is the Cu_1 only, which divides in the middle of the wing length into Cu_{1a} running to the wing-margin and a short Cu_{1b} towards the tip of the anal vein.

The anal veins are represented only by the first anal.

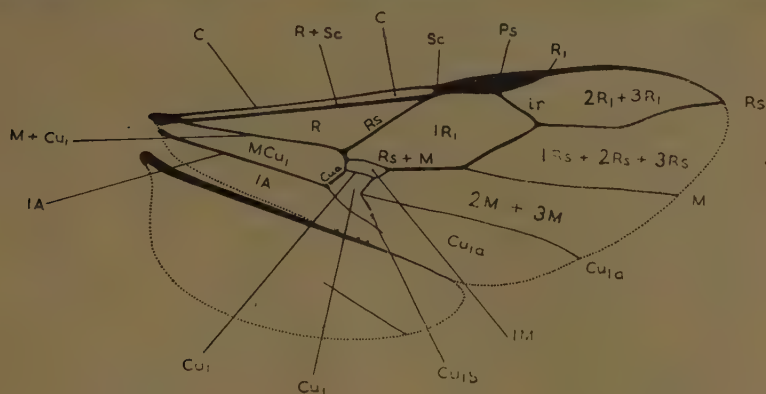
5. THE ABDOMEN.

The abdomen of Evanioidea resembles that of other Clistogastran Hymenoptera, being distinctly divided into a propodeum or first segment which is fused with the metathorax, and a gaster or functional abdomen which comprises the remaining segments. The propodeum has already been discussed as part of the thoracic mass, so that only the gaster will be here described together with its terminal appendages, the male genitalia and the ovipositor of the female. In the following account the strict morphological numbering of the abdominal segmentation will be referred to so that the propodeum is segment 1 and the gaster is numbered accordingly. Thus for instance the 4th segment refers to the 3rd segment of the gaster.

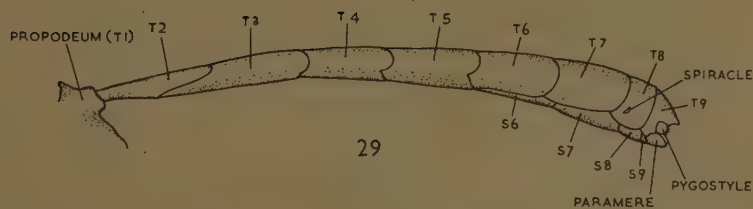
(a) *The Gaster.*

It is a diagnostic feature of the Evanioidea that the gaster is borne on the dorsum of the propodeum. It comprises eight distinct segments (the 2nd to 9th), with sometimes traces of a 9th and 10th. The form of the gaster is very variable; in *Gasteruption* it is long and gradually clavate (fig. 29) as in the Ichneumonidae, in *Aulacus* it is rounded and subelliptical (fig. 30), but in *Brachygaster* and *Evania* it is composed of a narrow petiole formed by the 2nd

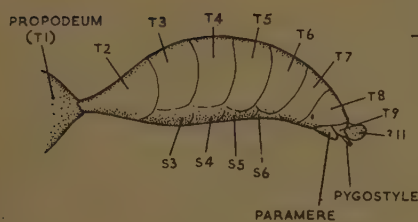
segment which bears an abrupt strongly laterally compressed club of the remaining segments (fig. 31). The 8th segment possesses a pair of functional spiracles,



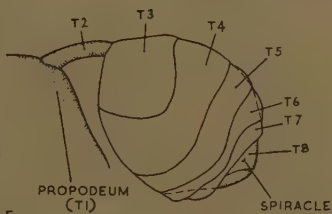
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29



30



31

FIGS. 28-31.—(28) Fore and hind wings of *Gasteruption* with the venation of the fore wing on Ross's nomenclature. Left lateral view of gaster of (29) *Gasteruption*. (30) *Aulacus*. (31) *Brachygaster*. T, terga, and S, sterna.

which together with the propodeal spiracles are the only respiratory openings of the abdomen. The terga (T) are greatly enlarged, especially in the EVANIIDAE and overlie the sterna (S) latero-ventrally. The tergum and sternum of each

segment are connected by a wide infolded membrane, the lateral conjunctiva, but there are no pleurites developed. The terminal segments differ in the two sexes. In the male the 8th sternum is small, and the 9th sternum reduced to a narrow transverse sclerite partly overlying the 8th; the 9th tergum is fairly well developed, but the 10th when present as in *Gasteruption* is invaginated under the 9th and very reduced: an eversible membranous bulb terminates the gaster in *Aulacus* and *Gasteruption* which bears the anus and is possibly the 11th segment (Snodgrass, 1941). The male genitalia are very compact, and partly withdrawn into the cavity between the 9th tergum and sternum, to which they are loosely attached by membrane. In the female (fig. 40 and 41) the 8th and 9th sterna are both divided into two lateral pieces, which are intimately united with the ovipositor and its valves. The 9th tergum consists of two large sides connected by a narrow band dorsally; posterior to this is a membranous bilobed projection which probably represents the 10th segment, with the anus opening between the supra-anal and sub-anal lobes. In both sexes two small lateral processes occur on the end of the 9th tergum probably derived from segment 10, and referred to by Snodgrass as the *pygostyles* or *socii*. These are rounded in *Gasteruption* and cercus-like in *Aulacus* and possess marginal hairs, (figs. 29 and 30).

(b) *The Abdominal Appendages:*

The appendages of the abdomen comprise the external copulatory structures and the egg-laying apparatus.

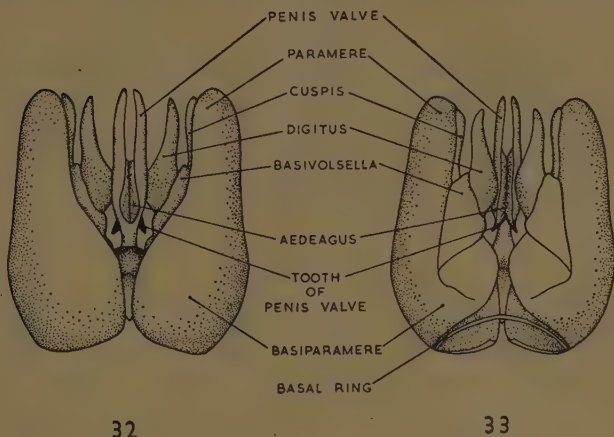
i. *The male genitalia.*—In the present work the male genitalia of *Gasteruption* and *Brachygaster* have been examined, while Snodgrass (1941) has described these in *Evania*.

It has been conclusively shown that the male genitalia of Hymenoptera are entirely phallic in origin. The phallus is loosely contained in the genital chamber at the end of the body and arises between segments 9 and 10. The structure of the phallus is fairly constant in the Order and no great difficulty exists in recognizing corresponding structures, but confusion has arisen owing to the multiplicity of terms employed in describing the latter. The phallic nomenclature used here is a slight modification of that recently proposed by Snodgrass, which has the advantage of avoiding the use of terms which also describe the mouthparts. Note will be made in the following account of the most commonly encountered synonyms.

The phallus is well sclerotized, almost quadrate in form in *Gasteruption* (fig. 32), and elongate in *Brachygaster* (fig. 38). It consists essentially of a median aedeagus which is the intromittent structure receiving the ductus ejaculatorius, and which is surrounded by the caulis and its processes. The caulis is formed of two segments, the basal ring and the basiparameres. The *basal ring* (cardo, lamina annularis, gonocardo) is broad and complete in *Evaniidae*, but is very reduced, narrow and incomplete dorsally in *Gasteruption* (figs. 33 and 38). Commonly in the latter the upper part of the ring fuses with the basiparameres so as to form a flange on each of these. As the phallus is orientated longitudinally the ring encircles a foramen which is directed anteriorly.

The 2nd segment of the caulis comprises the basiparameres and basivol-sellae, which bear distally the parameres and the volsellar lobes respectively. The *basiparameres* (stipites, laminae paramerales, gonostipites) appear to be

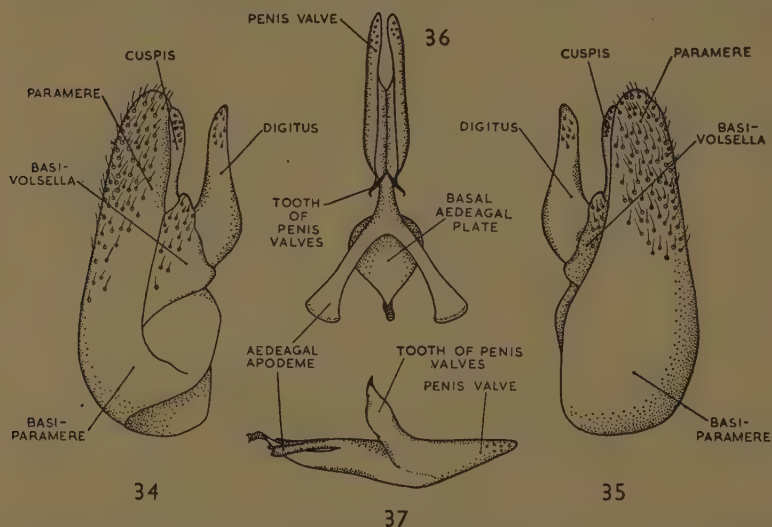
simply the enlarged bases of the parameres, but the continuity arises because the latter are outgrowths of the caulis. In many Hymenoptera a hinge exists between paramere and basiparamere but in Evanioidea no such line exists, although the sclerotization will break along a line of weakness. Dorsally the parameral plates are united by a narrow strip of membrane which in *Brachygaster* has become occluded so that the basiparameres lie adjacent to one another (fig. 38). In *Gasteruption* the dorsal part of the basiparameres is closely united with a dorsal plate developed at the base of the aedeagus. The ventral part of the basiparamere is smaller than the dorsal and united with the basivolsella, a separate and distinct sclerotization of the caulis. The *parameres* (harpes, squamae, gonosquamae) are the distal continuations of the basiparameres being formed as prolongations from the caulis, and are rounded in *Gasteruption*



FIGS. 32, 33.—Male genitalia of *Gasteruption jaculator*. (32) Dorsal view. (33) Ventral view.

(figs. 32 and 33) but pointed in *Brachygaster* (figs. 38 and 39). At the tip each bears a number of bristles. The volsella as a whole comprises a basal plate or *basi-volsella* united with the basiparamere and two terminal volsellar lobes. The basivolsellae are subtriangular in *Gasteruption* (figs. 33 and 34), and elongate and rectangular in *Brachygaster* (fig. 39); they are sclerotizations in the ventral wall of the caulis on the inner sides of the basiparameres. The volsellar lobes are borne on the distal end of each basivolsella; the outer one or *cuspis* (distivolsella of Peck) is a direct extension of the basivolsella itself, while the inner or *digitus* (Gonolacinia of Peck, Sagitta of Pratt) is movably articulated with the latter. They lie close against the distal end of the aedeagus, and are hence referred to by Crampton as the copulatory ossicles. The *cuspis* in *Gasteruption* (fig. 34) is long and narrow, slightly thickened at the apex, but in *Brachygaster* (fig. 39) is large and leaf-like and surrounds the digitus. The latter in both genera is a curved structure, broad at the base and pointed apically which partly underlies the aedeagus. The *aedeagus* (penis) is the primary median reproductive structure and receives the end of the ductus ejaculatorius. It is

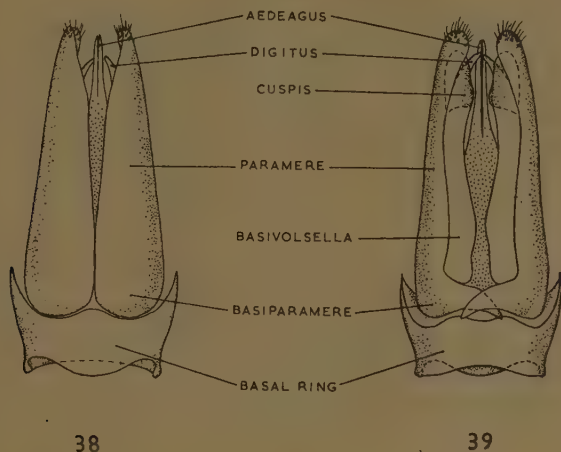
evidently of twofold origin and opens ventrally by a long median slit, but there is also a dorsal groove. The walls of the aedeagus are developed as a pair of elongate lateral *penis valves* (laminae aedeagales, sagittae), which project freely for a variable length at their distal ends. The basal part of the aedeagus of *Brachygaster* is not highly differentiated and even largely membranous, but *Gasteruption* exhibits some most bizarre developments which show well-marked specific differences. Anteriorly the proximal ends of the penis valves are drawn out into two strong divergent arms, the *aedeagal apodemes* (parameres of Peck), which terminate just inside the basiparameres. These apodemes are a common feature of the Hymenopterous phallus, but in *Gasteruption* there is developed on



FIGS. 34-37.—*G. jaculator*. Right half of caulis of male genitalia with their processes. (34) Ventral view. (35) Dorsal view. (36) Ventral view of aedeagus. (37) Left lateral view of aedeagus; the tooth of the penis valves is ventral.

the dorsal side at the point of bifurcation a large anteriorly directed plate (fig. 36). This plate is slightly convex dorsally and concave ventrally and assumes various shapes in the different species; thus in *G. jaculator* and *G. minutum* it is acuminate anteriorly (more strongly pointed in the latter than the former), but is bilobed in *G. assectator*. No similar structure appears to have been described in the Hymenoptera, and the name *basal aedeagal plate* is here proposed for a development that may prove of use in separating some of the closely allied species in the genus; it is, however, possible that the plate corresponds with the very small basal lobe of the penis which Duncan mentions as occurring in *Vespula pennsylvanica*. A second extraordinary development of the aedeagus is found in the middle of its length as a large ventrally directed tooth (fig. 37), which is formed by two fused processes from the bases of the penis valves. The distal end of the tooth is slightly forked and betrays a

double origin. Like the basal aedeagal plate the proximal tooth of the penis valves varies in shape and size in different species of *Gasteruption*; in the closely similar *G. minutum* and *G. assectator* it is quite short and directed antero-ventrally, but in *G. jaculator* it is very large and directed ventrally. There is some likelihood that with wider study the nature of the tooth could be used to distinguish "species-groups" within the genus, for there are also associated differences in the lengths of the free apices of the penis valves; for example in those species with a short blunt tooth the free extremities of the valves are short, whereas they are long in forms with a large pointed tooth. The male genitalia of *Evania* as figured by Snodgrass (1941) are essentially very similar to those of *Brachygaster*. The parameres, basiparameres, basivolsellae, basal



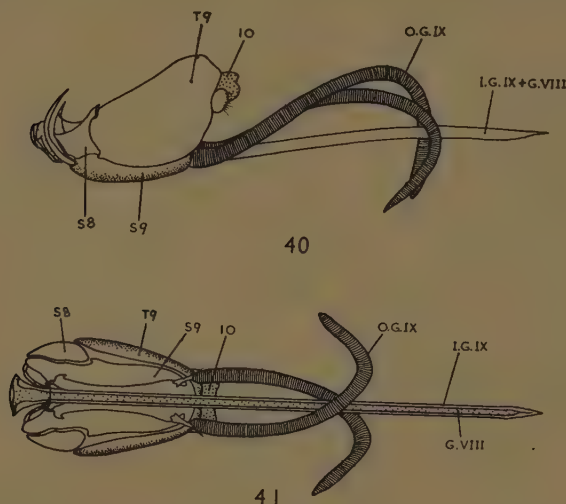
FIGS. 38, 39.—*Brachygaster minutus*, male genitalia. (38) Dorsal view, (39) Ventral view.

ring and aedeagus are particularly alike, but there are minor differences in the form of the volsellar lobes. The cuspis and digitus are both narrow at the base in *Evania*, but broad in *Brachygaster*, while the digitus is pointed in the latter genus and directed towards its opposite number; in *Evania* the digitus is angled terminally and directed towards the cuspis of its own side.

ii. *The ovipositor* (figs. 40 and 41).—The ovipositor of the female is long and adapted for piercing. In Evanioidea as other Parasitica it retains the primary function of egg-laying and is not modified as a sting. In the Evaniidae it lies within the overlapping terminal tergites of the gaster and is not visible externally, but in the Gasteruptionidae and Aulacidae it is exerted and often as long as the whole body. The ovipositor of *Gasteruption assectator* is of moderate length, and has been employed below to typify the general structure of the organ in the Evanioidea.

The ovipositor emerges from the ventral side of the end of the gaster which has become accordingly modified; the 8th and 9th sterna of the abdomen are both divided into two lateral pieces, which are closely associated with the

proximal ends of the ovipositor valves. Each lateral 8th sternite or 1st valvifer is subtriangular and articulates with one of the first pair of valvulae; the latter are the gonapophyses of the 8th segment (G. VIII), and lie closely parallel forming the side-walls of the terebra or median part of the ovipositor; they correspond with the stylets of the sting of higher Hymenoptera. Each piece of the divided 9th sternum is elongate, and articulated proximally by a small process with one of the pair of 2nd valvulae; the 2nd valvulae are the inner gonapophyses of the 9th segment, and are fused along their length to form a single valve which overlies the gonapophyses of 8 and corresponds with the stylet-sheath of a bee or wasp. A third pair of valvulae occurs articulated to



FIGS. 40, 41.—Ovipositor and end of gaster of *Gasteruption assectator*. (40) Left lateral view. (41) Ventral view. *T*, terga; *S*, sterna; *I.G. IX*, inner gonapophysis of segment 9 or stylet-sheath; *O.G. IX*, outer gonapophysis of segment 9 or third valvulae; *G. VIII*, gonapophysis of segment 8 or stylet.

the distal ends of the 9th sternites or 2nd valvifers as Snodgrass terms the latter; these valves are the outer gonapophyses of segment 9. They are as long as the other gonapophyses and in life lie very closely adpressed to these, so that the median terebra of the ovipositor is normally obscured from view. In the illustrations the 3rd valves are opened out to show the others.

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PART II.—THE TAXONOMY AND BIOLOGY OF THE BRITISH EVANIOIDEA.

With 31 Text-figures.

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1. INTRODUCTION.

The Evanioidea comprise a small group of parasitic Hymenoptera which has been sadly neglected by monographers. No account of them exists in English, and formerly identification was only possible by reference to rather old foreign publications. The present work is therefore an attempt to remedy such deficiency by providing reliable keys for the identification of the British species, descriptions of each of the latter, and an accurate check list. There has also been appended to the description of each species notes on the distribution of the form and as much information as can be obtained on the biology.

The greatest works on the Evanioidea are the monographs of the world's species of Schletterer (1889) and of Kieffer (1912). Unfortunately these are now rather out of date, and in the latter case there is often some doubt concerning the validity of a number of the species included. This is especially true of the genus *Gasteruption*, but there is fairly universal agreement upon *Aulacus* and the EVANIIDAE (EVANINAE of Kieffer). The latter author saw very few types of the species of *Gasteruption*, and included forms as different

species if there were any slight discrepancies in the original descriptions. Recently (1946) Ferrière in his paper on the Swiss species of *Gasteruption* has, however, been able to clear up much of the complex synonymy, as he has examined the types of Tournier's species. After examining the literature already cited and a reference by Roman (1932) to the valid name for *G. jaculator* the writer believes the specific names and synonymy employed later to be correct.

The British species were first listed by Marshall (1872); he included five species which appear also in the present list, and two others which are rejected by the writer. The first of these, *Evania fuscipes*, has since been shown to be synonymous with *E. appendigaster*, while *Gasteruption erythrostomum* Marshall was included on the strength of a record by Westwood (1843) of a capture at Highgate; the specimen in question (Oxf. Mus.) has been examined and shows no differences from the common *G. jaculator*. Waterston (1928) has listed six British species of *Gasteruption*, viz., *G. thomsoni*, *G. foveolum*, *G. pedemontanum*, *G. terrestre*, *G. abeillei*, and *G. assectator*, but regrettably with no further information. Morley (1937) rejects Waterston's list as it is unsubstantiated, but Kloet and Hincks (1945) have used it as the basis of their check list and added *G. rugulosum* (record: *Vict. County. Hist., Cambs.*) and a doubtful *G. tournieri*. In the present work *G. abeillei* and *G. rugulosum* are not admitted for reasons given later, *G. pedemontanum* and *G. terrestre* are shown to be synonyms, and *G. minutum* has been added; there are therefore now five fully accepted British species of *Gasteruption* and two doubtful species, *G. rubicans* being admitted with a question-mark as *G. tournieri*.

With regard to the habits and life-histories of the British Evanioidea the paucity of information is even more marked than in the taxonomy. Schletterer and Kieffer in their monographs have provided some knowledge, and Höppner (1904) has given an account of the life-history of *Gasteruption*, but much of the information given in the following pages has been accumulated by examination of all the data labels on the specimens in the collections studied.

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Dr. John Smart, Zoological Laboratory, Cambridge, for the loan of the Cambridge Collection to Dr. Richards for the writer's use. Reference to the Cambridge Collection is abbreviated later to Cambs. Mus.

Professor G. C. Varley, Hope Department of Entomology, Oxford University Museum, for the loan to Dr. O. W. Richards of the Oxford Collection of Evanioidea for the use of the writer. Specimens in this collection when referred to later are appended Oxf. Mus.

The scientific names of all plants referred to have been taken from the Check-List of British Vascular Plants issued by the British Ecological Society, (1946, *J. Ecology* **33**: 308-347).

2. CHARACTERISTICS OF THE EVANIOIDEA.

The Evanioidea are a super-family of Hymenoptera Parasitica separable from the rest of the Order by combination of the following characters :

Antennae 13 segmented in the male, 14 in female ; not肘ed. Maxillary palpi 6, labial palpi 4 segmented. 3 ocelli disposed in a triangle. Pronotum extending back to tegulae, more or less covered by large mesonotum ; metanotum very short. Forewings with distinct costal cell ; venation of hindwings almost obsolete. Trochanters 2-jointed. Propodeum large, with the abdomen (gaster) inserted on the dorsum ; abdominal sternites strongly chitinated.

3. KEY TO THE FAMILIES OF EVANIOIDEA.

1. Forewings with two recurrent nervures (r, fig. 1), three closed discoidal cells, and three submarginal (cubital) cells ; antennae inserted low down, on a line with lower margins of the eyes, which are remote from the mandibles 1. Fam. AULACIDAE.
- Forewings with one recurrent nervure or none, third discoidal cell open to wing-margin or absent, two submarginal cells or none ; antennae inserted high up, about on a line with middle of eyes, which are approximated to, or remote from, the mandibles 2.
2. Abdomen of a slender abrupt petiole, which is almost as long as the remaining segments, which form a laterally compressed ovate body ; ovipositor not exerted ; eyes remote from mandibles ; head not prolonged behind eyes ; propleura short 2. Fam. EVANIIDAE.
- Abdomen long and gradually clavate ; ovipositor exerted ; eyes approximated to base of mandibles ; head prolonged behind eyes ; propleura long, forming a "neck" 3. Fam. GASTERUPTIONIDAE.

4. (1) Family AULACIDAE.

Head roundish, as wide as thorax, and strongly arched anteriorly ; not narrowed behind eyes, which are circular and remote from mandibles. Antennae inserted low down on head, on a level with lower margin of eye ; scape short. Mandibles short and broad, tridentate. Propleura short. Mesonotum raised anteriorly, strongly transversely rugose, and distinctly divided. Fore wings with three submarginal and three discoidal cells, and two recurrent nervures. Abdomen elliptical and sub-compressed, borne on a pyramidally raised propodeum ; ovipositor long and exerted.

The AULACIDAE are represented in Britain only by the genus *Aulacus*, which can therefore be distinguished by the above family description, and which is also applicable to the single species.

1. *Aulacus striatus* Jurine, 1807.

A. arcticus Dahlbom, 1837 ; *A. exaratus*, Giraud, 1850.

Length.—7-9 mm.

Head black, smooth and shining, with clypeus red or reddish yellow. Distance from eye to posterior ocellus equal to that between posterior ocelli.

Antennae very long, with scape thickened.

Thorax black and very strongly sculptured ; mesonotum transversely wrinkled, propodeum reticulately wrinkled. Wings not maculated, and hind wing with two hamuli. Legs black or reddish, front and middle femora paler ; coxae finely striated. Abdomen black basally and apically, but largely suffused with red in the middle region. Ovipositor as long as or longer than the abdomen ; valves entirely black.

Distribution.—As a British insect *Aulacus striatus* is exceedingly rare; no published records of its occurrence exist, and the number of specimens in collections is severely limited. Recently (1949), however, a small number have been taken at Mundford, West Norfolk.

The range abroad includes most of Northern and Central Europe, from France, eastwards to Russia, and north to Lapland, but not, apparently, Germany.

Biology.—The ovaries of *A. striatus* are pyriform in shape, each being 1.25 mm. long by 0.6 mm. thick, and containing some 200 eggs. The eggs when mature are pedunculate, and 0.64 mm. in length. The body of the egg is almost spindle-shaped, appearing opaque, and measuring 0.14 mm. long and 0.07 mm. in thickness; the stalk is almost transparent, attenuated and thread-like,



FIG. 1.—*Aulacus*. Fore and hind wings. 1, marginal cell; 2, first submarginal cell; 3, second submarginal cell; 4, third submarginal cell; 5, first discoidal cell; 6, second discoidal cell; 7, third discoidal cell; r, recurrent nervures.

0.5 mm. in length, and only 0.01 mm. thick. The larva lives in rotten tree-trunks, where it is parasitic upon Coleopterous larvae (chiefly CERAMBYCIDAE) and Hymenopterous larvae, the latter including those of *Xiphydria camelus* (L.) and *X. prolongata* (Geof.) (= *X. dromedarius* (Fab.)). The structure of the larva, and whether it lives within or outside the host-larva, remains to be investigated. The pupa is white and enclosed within a cocoon. Imagines have been found on timber containing eggs of *X. prolongata*, and have been observed on the blossoms of UMBELLIFERAE.

5. (2) Family EVANIIDAE.

Head as broad as the thorax, not prolonged behind the eyes, which are sub-elliptical and remote from the mandibles. Mesonotum small and depressed, prothorax not elongate. Abdominal attachment remote from the scutellum, and by a slender petiole which is almost as long as the remaining segments together, these forming a strongly laterally compressed, broad, ovate body, the entire abdomen being shorter than the head and thorax. Ovipositor not exerted.

The two British species in the family are in separate genera, but no definition of these will be given, as this would involve needless repetition in the following accounts of these two species.

(5a) Key to the British Species of EVANIIDAE.

1. Venation of fore wing well developed, with submarginal and discoidal cells; scape of antenna long; hind wing with 10 hamuli; length 8 mm. 1. *Evania appendigaster* (L.)
- Venation of fore wing very reduced, no submarginal and discoidal cells, scape of antenna short; hind wing with 4 hamuli; length 3-4 mm. 2. *Brachygaster minutus* (Olivier).

(5b) Descriptions of the British Species of EVANIIDAE.

1. *Evania appendigaster* (Linnaeus, 1758).

E. laevigata Olivier, 1791; *E. fuscipes* Illiger, 1817.

Length.—8 mm. Entirely black.

Head shining, microscopically finely punctured, without furrows below antennae; malar area large, equal to half the length of eye; mandible with two teeth. Scape very long; in male a little longer than two following segments together, in female nearly as long as three following together; 3rd segment four times as long as 2nd, 4th three times as long as 2nd, in male; 3rd three times and 4th twice as long as 2nd in female.

Prothorax very short; mesonotum shining, almost smooth, except for diffuse microscopic puncturation and one or two larger punctures; prescutum separated from scutum by deep lateral grooves; parapsidal furrows distinct; scutellum with scattered shallow punctures; mesopleura almost smooth; metapleura strongly and closely punctured. Propodeum with large shallow reticulate punctures with a tendency to lie in transverse rows. Boundary of propodeum with metapleuron marked by a regular horizontal row of shallow dorsoventrally elongated depressions. Fore wings with one recurrent nerve, one small closed submarginal cell, very large 1st discoidal cell, and 3rd discoidal cell open to wing margin; each wing with large pointed anal lobe; hind wings each with 10 hamuli. Hind coxae with a few scattered punctures, and hind legs nearly twice as long as the body. Abdomen shining, "club" sometimes reddish ventrally, strongly compressed laterally, triangular or almost ovate. Ovipositor not exerted.

Distribution.—No localities of capture of British specimens are known to the writer.

Abroad this species is world-wide, though it only seldom occurs in Europe.

Biology.—*Evania* lays its eggs within the oothecae, prior to their hardening, of Cockroaches (BLATTIDAE), including *Pertplaneta americana* (L.) and *Blatta orientalis* L. The parasite-larva develops and pupates within the ootheca, which is utilized as a cocoon. The adult emerges in summer, and may be found visiting flowers, among which are *Petroselinum crispum* (Mill.) and *Foeniculum vulgare* Mill. Cros (1942), in Spain, investigated the life-history of the closely allied, though non-British, *E. punctata*, and found that only one adult parasite emerged from the capsule, and that there were at least two generations in a year, one in June or July, and a second in September or October.

2. *Brachygaster minutus* (Olivier, 1791).

Hyptia minuta Rossi, 1807, *B. fulvipes* (Curtis, 1829).

Length.—3-4 mm.

Head black, closely and strongly punctured, with fine transverse striations between the

punctures; narrow curved ridge from inner eye-margin to base of mandible, and two vertical furrows from bases of antennae to mandibles; malar area large, as long as first two antennal segments together; mandibles red apically. Distance between posterior ocelli twice as great as that between posterior ocellus and eye. First antennal segment (scape) in male a little longer than 2nd and 3rd but considerably shorter than 2nd to 4th segments together; female with scape as long as 2nd to 4th segments together; male with 4th segment one and a half times as long as, in female equal to, 3rd.

Thorax black, closely set with large shallow punctures, except on dorsal parts of mesopleura, which are obliquely wrinkled; mesonotum slightly roughened, pleura and propodeum smooth, between the punctures; parapsidal furrows distinct. Fore wings with only three complete cells; no submarginal or discoidal cells; hindwings each with four hamuli and an acuminate anal lobe. Legs black or dark brown, except for the front and middle tibiae of the female, which are yellow.

Abdomen black or dark red, formed of a narrow petiole bearing a laterally compressed, ovate, or sub-triangular body. Ovipositor not exerted.

B. minutus is the smallest European Evaniid, and unlikely to be mistaken for any other British insect.

Distribution.—British records are few: Reigate, Surrey (Chitty), and Shere, Surrey (Capron); Feldon, Herts (Piffard); and Sandown, Isle of Wight (E. A. Butler). Other specimens have been taken in the New Forest (S. Hants), at Exmouth (S. Devon), and at Studland and Piddletrenthide (Dorset).

The species is widely distributed over the whole of Europe.

Biology.—*Brachygaster minutus* imagines occur in July and August on bushes, low plants, or among marram-dunes on the coast, usually in situations where cockroaches are likely to occur; specimens have been taken on *Asparagus officinalis* L. (LILIACEAE). As is the case with *Evania* the eggs are laid in cockroach oothecae, though of different species, viz., *Blatella germanica* (L.) and *Ectobius lapponicus* (L.).

6. (3) Family GASTERUPTIONIDAE.

Form slender. Occipital part of head hemispherical or sub-conical; hind-margin sharply ridged or reflexed, sometimes with depressions. Eyes large and elliptical, almost reaching the mandibles. Antennae inserted on a level with the middle of the eyes; scape short. Propleura long, forming a "neck." Mesonotum large and rounded anteriorly. Metanotum short. Propodeum reticulate. Posterior tibiae strongly clavate. Fore wings with long marginal cell almost reaching wing-margin at the apex. Two submarginal cells, first very large and second open to wing-margin. First discoidal cell very small and narrow. Second discoidal cell open behind by a deflection of the anal nervure. Third discoidal cell open to the wing-margin. Abdomen elongate, gradually increasing in width from its point of insertion, and sickle-shaped. Ovipositor exerted, sometimes short but usually very long.

As only the genus *Gasteruption* is represented in the British Isles the above description will suffice for the genus as well as the family. The genus *Trichofoenus* has been separated from *Gasteruption* on the ground that the eyes are hairy and not glabrous, but little reliance can be placed on this generic difference, as undoubted British specimens of *G. assectator* have occurred with pubescent eyes.

For many years the genus *Gasteruption* was known as *Foenus* Fabricius, 1798, but as was pointed out by Schletterer, the valid name on the basis of priority must be *Gasteruption* Latreille, 1796. Owing to the writings of Semenov the

name *Gasteruption* has also become established in the literature, while Comstock refers to the family as the *Gasteruptionidae*.

As a result of the present work there appear to be five species of *Gasteruption* which can be fully accepted to the British list, and two others for which insufficient data exists.

(6a) Key to the British Species of *Gasteruption*.

1. Males.

1. Occipital margin of head with a distinctly raised reflexed collar; mesonotum reticulate 2.
- Occipital margin of the head sharp but not reflexed; mesonotum shagreened or (*G. rubricans*) granulate 5.
2. Head without depressions in front of collar; 2nd antennal segment equal in length to 3rd 1. *G. jaculator* (L.)
- Head with one or three depressions in front of collar; 3rd antennal segment longer than 2nd except in *G. tournieri*. 3.
3. Head with one depression in front of collar. 2. *G. foveolum* Szépligeti.
- Head with three depressions in front of collar. 4.
4. Median depression deep and sharply defined anteriorly (fig. 12). 3. *G. pedemontanum* (Tournier).
- Median depression shallow and not sharply defined anteriorly (fig. 9); 2nd and 3rd antennal segments equal in length [4. *G. tournieri* Schletterer].
5. Mesonotum granulate; mandibles and legs red [5. *G. rubricans* (Guérin)].
- Mesonotum shagreened; mandibles black, legs mainly black. 6.
6. Distance between eye and mandible equal to the width of the mandible at the base, or to length of 1st antennal segment; front and middle tibiae almost entirely black 6. *G. minutum* (Tournier).
- Distance between eye and mandible distinctly shorter than width of mandible at base, or than the 1st antennal segment; front and middle tibiae red 7. *G. assectator* (L.).

2. Females.

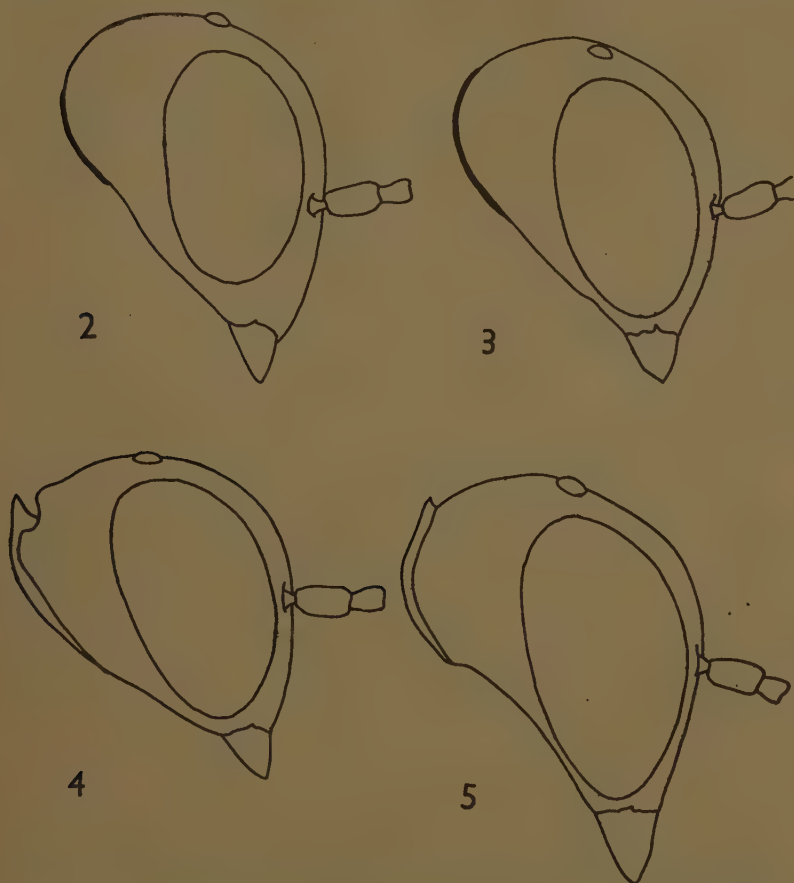
1. Ovipositor as long as the whole body; occipital margin of head with a reflexed collar 2.
- Ovipositor shorter than the abdomen; occipital margin of head narrowly raised but not forming a reflexed collar. 5.
2. Head without depressions in front of collar. 1. *G. jaculator* (L.)
- Head with one or three depressions in front of collar 3
3. Head with one median depression in front of collar 2. *G. foveolum* Szépligeti.
- Head with three depressions in front of collar 4.
4. Median depression deep, sharply defined anteriorly (fig. 12.); outer side of front tibia largely black 3. *G. pedemontanum* (Tournier).
- Median depression shallow, not sharply defined anteriorly (fig. 9); outer side of front tibia entirely white [4. *G. tournieri* Schletterer.]
5. Head and thorax almost entirely red; mesonotum granulate [5. *G. rubricans* (Guérin)].
- Head and thorax black; mesonotum shagreened 6.
6. Distance from eye to mandible equal to width of mandible at the base; ovipositor equal in length to 1st abdominal segment. 6. *G. minutum* (Tournier).
- Distance from eye to mandible distinctly shorter than width of mandible at the base; ovipositor one and a half times as long as 1st abdominal segment 7. *G. assectator* (L.).

(6b) Descriptions of the British Species of *Gasteruption*.

(1) *Gasteruption jaculator* (Linnaeus, 1758).

G. granulithorax (Tournier, 1877), *G. oblitteratum* (Abeille de Perrin, 1879), and *G. thomsoni* Schletterer, 1885.

Ferrière, after examining Tournier's types and specimens determined as *G. thomsoni*, and specimens identified as *G. oblitteratum* Abeille, concluded that the names were all synonymous. Roman (1932) established that the Linnaean type of *Ichneumon jaculator* belonged to the species afterwards redescribed as *Gasteruption thomsoni* by Schletterer.



FIGS. 2-5.—*Gasteruption*. Lateral view of the head. (2) *G. minutum*; (3) *G. assectator*; (4) *G. pedemontanum*; (5) *G. jaculator*.

Length.—Male 8–13 mm., female 10–15 mm.

Head dull black, finely transversely striated, and with a reflexed semi-translucent occipital "collar," not preceded by any depressions; malar area very short, eye almost reaching base of mandible; distance between posterior ocelli distinctly greater than that between a posterior ocellus and the eye. Male antennae with 3rd segment equal in length to 2nd (fig. 14), 4th distinctly longer than 2nd and 3rd together; female with 3rd segment twice as long as 2nd, 4th equal in length to 2nd and 3rd together. Thorax dull black; pronotum with V-shaped row of elongate punctures on each side; propleuron (neck) finely striated; mesonotum strongly transversely wrinkled, less distinctly so on the parapsides; propodeum strongly reticulately wrinkled, more strongly in the female than the male. Middle and hind coxae finely transversely striated in the male; only hind coxae in female. Legs usually paler in male than female; front and middle tibiae yellow at base; hind tibiae with a white or yellow incomplete ring towards the base; hind tarsi completely dark in male, with the 1st segment white or yellow in female.

Abdomen black with orange-red marks of variable extent; in the female commonly almost the whole of tergites 2–4 and sometimes also 5 are red, while in the male this colour is usually localized at the junctions of tergites 2–5. In the male genitalia the parameres are almost parallel-sided, the free apices of the penis-valves are long, the proximal tooth of the penis-valve is very large (*ptv*, fig. 31), and the basal aedeagal plate (*ap*, fig. 27) is acuminate anteriorly. Ovipositor in female usually equal in length to whole body, or occasionally slightly longer or shorter; valves black with apices white.

G. jaculator can be distinguished from other British species by the reflexed collar, combined with the absence of occipital depressions, the lengths of the antennal segments, and the development of red on the abdomen of female.

Distribution.—*G. jaculator* is certainly the commonest species of the genus in the British Isles, being known from the following counties and vice-counties: London, Surrey, North and South Essex, East and West Kent, Bucks, Oxford, Cambridge, Berks, East and West Suffolk, West Norfolk, East and West Gloucester, South Hants, Dorset, Sussex, North and South Devon, Warwick, Leicester, and Staffs—i.e., it is widely distributed over the southern and south midland regions of England.

Abroad this species spreads over the whole of Northern and Central Europe.

Biology.—Imagines of *G. jaculator* may be found from June to September visiting flowers, particularly Umbelliferae such as *Daucus carota* L., *Heracleum sphondylium* L., *Chaerophyllum temulum* L., *Angelica sylvestris* L., *Aegopodium podagraria* L., *Pimpinella saxifraga* L., *Pastinaca sativa* L., and also sometimes Labiates such as *Mentha* sp., and Compositae such as *Carduus*. It has also been taken on Beech and exploring the burrows of wood-boring beetles in dead Oak, while it has been bred from a stump containing a nest of the bee *Chelostoma florissomne* (L.). Morley (1937) records it as ovipositing in the burrows of *Pemphredon lugubris* (Fab.) (SPHECIDAE). Parasitizes a number of species of *Prosopeis*, *Osmia* and *Odynerus* (Höppner, 1904, and Ferrière, 1946).

(2) *Gasteruption foveolum* Szépligeti, 1903.

Length.—11 mm.

Head black, transversely striated; hind margin strongly curved and with a reflexed collar, in front of which is a single median depression (fig. 7); malar area short; distance between posterior ocelli greater than that between posterior ocellus and eye. Third antennal segment considerably longer than 2nd in male, twice as long in female; 4th shorter in female, longer in male, than two preceding segments together.

Thorax black; pronotum with shallow punctures and well developed pronotal processes; propleuron shagreened, tending to striate, not so strongly as *G. jaculator*; mesonotum closely transversely wrinkled, equally distinctly on parapsides; propodeum reticulate, weaker than in *G. jaculator*. Hind coxae shagreened; legs dark, except for proximal end of hind tibia, and 1st segment of hind tarsus, which are white.

Abdomen black, hinder half of segments 2, 3, and 4 red. Ovipositor equal in length to the body; distal ends of valves white.

G. foveolum is unlikely to be confused with any other British species, except *G. jaculator*, from which it may be distinguished by the indented hind-margin of the head, the lengths of the antennal segments in the male, the presence of an occipital depression, and the weaker and more regular sculpture of the thorax.

Distribution.—The inclusion of this species in the British list rests upon a single female taken on the underside of a Birch leaf on Thursley Common, Hindhead, Surrey (Waterston, 1928). Examination of this specimen (B. M. Coll.) leaves no doubt that it is of *G. foveolum*, for it may be distinguished from the only other European species (*G. foveolatum* and *G. laticeps*) with a single occipital depression by the malar area being shorter than the 2nd antennal segment, the ovipositor being equal in length to the body, and the white hind metatarsus.

Biology.—Nothing known; the British specimen was taken on August 26th.

(3) *Gasteruption pedemontanum* (Tournier, 1877).

G. terrestre (Tournier, 1877).

Tournier's types of *G. pedemontanum* and *G. terrestre*, differing only in the sculpture of the mesonotum, have been examined by Ferrière (1946), who believes them to be specimens of the same species.

Length.—10–16 mm.

Head black, semi-shining, strongly contracted behind the eyes, and finely transversely striated; reflexed collar large, preceded by a deep median depression sharply defined anteriorly (especially in the female), and a shallow lateral depression on each side (figs. 4 and 12); malar area very short; distance between posterior ocelli almost twice that between posterior ocellus and eye. Third antennal segment one and a half times as long as 2nd in male, twice as long in female; 4th segment nearly as long as first three together in male, equal in length to 2nd and 3rd together in female.

Thorax dull black; pronotum with shallow elongate punctures and very distinct pronotal processes; propleuron strongly striated; mesonotum, mesopleuron, metapleuron and propodeum reticulately punctured; sculpture tending to transverse wrinkling on sides of prescutum, and particularly on parapsides. Hind coxae finely wrinkled; legs dark, except for white ring at base of hind tibia, and white dorsal side of 1st segment of hind tarsus in female.

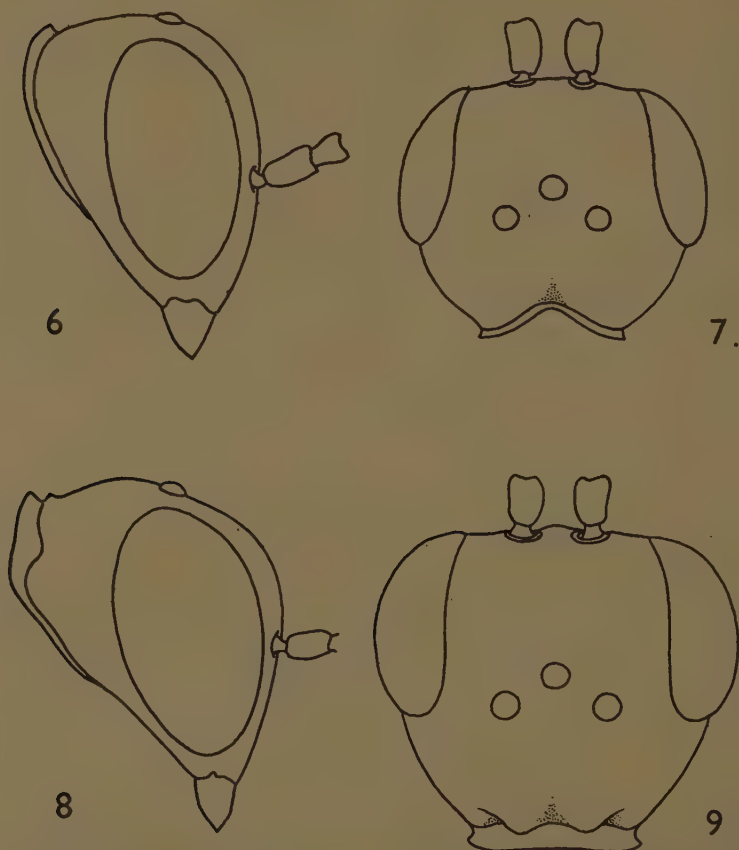
Abdomen black with distal ends of segments 2, 3, and sometimes 4, red in male, and almost the whole of segments 2 and 3 orange-red in female. Ovipositor as long as the whole body; apices of valves white.

Distribution.—This species is only known from South Devonshire, where a number of specimens, chiefly female, have been taken at Lustleigh, Newton Abbot and Bovey Tracy.

Abroad its range includes the whole of Central and Southern Europe, east to Persia and Armenia.

Biology.—No records of the habits of *G. pedemontanum* exist for Britain, but on the Continent adults occur between June and August on flowers of UMBELLIFERAE such as *Petroselinum crispum* (Mill.), *Pimpinella saxifraga* L., *Anthriscus sylvestris* (L.), *Heracleum sphondylium* L., and *Daucus carota* L., Compositae such as *Solidago canadensis* L., and various species of *Euphorbia*.

The larvae are parasites in nests of bees of the genus *Osmia*.



FIGS. 6-9.—*Gasteruption*. Lateral and dorsal aspects of head. (6) *G. foveolum*; (7) *G. foveolum*; (8) *G. tournieri*; (9) *G. tournieri*.

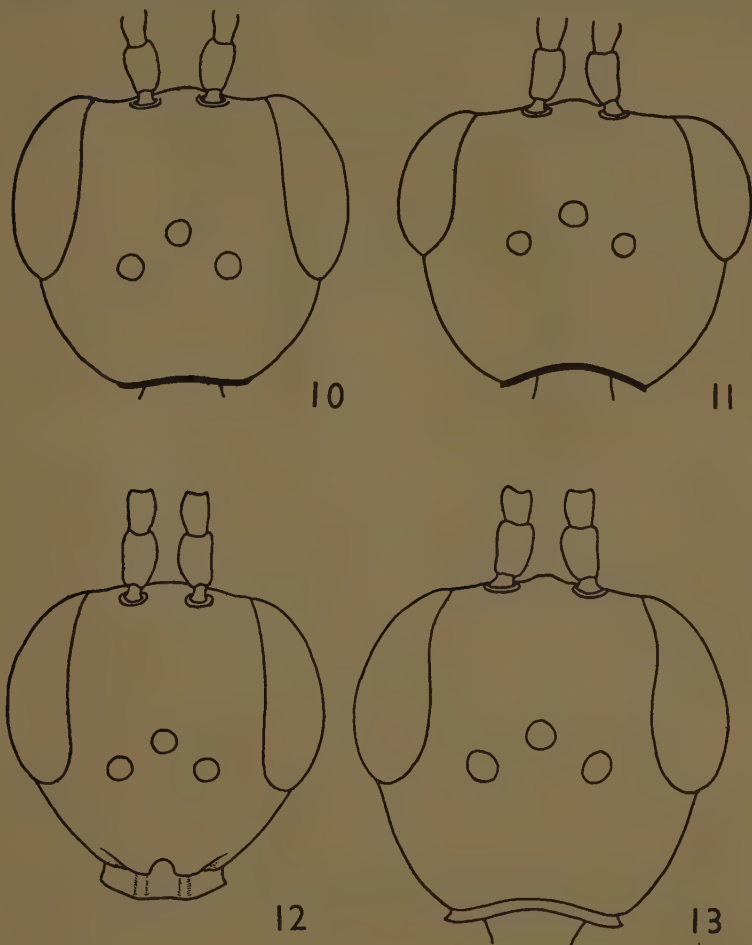
[(4) *Gasteruption tournieri* Schletterer, 1885.]

G. jaculator (Tournier, 1877).

Length.—8-10 mm.

Head shining black, almost smooth, strongly contracted behind eyes, which are approximated to the mandibles; well-developed reflexed collar and three occipital depressions, the median depression shallow and not sharply defined anteriorly (fig. 9); distance from

eye to posterior ocellus less than that between posterior ocelli. Third antennal segment about equal in length to the 2nd in male, twice as long in female; 4th in male nearly as long as three preceding together, in female as long as two preceding segments together.



FIGS. 10-13.—*Gasteruption*. Dorsal views of head. (10) *G. assectator*; (11) *G. minutum*; (12) *G. pedemontanum*; (13) *G. jaculator*.

Thorax black; pronotum with strong processes and shallow punctures; propleuron striated. Mesonotum transversely wrinkled and punctured, less distinctly on the sides of scutum and parapsides; mesopleuron, metapleuron and propodeum strongly reticulately punctured. Legs dark reddish, except for outer side of front tibia, base of middle tibia, ring at base of hind tibia, and hind metatarsus of female, which are white.

Abdomen black, red at the junctions of tergites 2-6 in male, and with smaller red marks

at junctions of tergites 2-5 in female. Ovipositor equal in length to the body with valves white at the tip.

G. tournieri is distinguishable from *G. pedemontanum* by the shallow median fossa of head, sculpture of mesonotum, white outer edge of front tibia, and the smaller size.

Distribution.—There is no undoubted occurrence of this species in Britain. A specimen of *Gasteruption* in the collection of L. A. Carr (Oxf. Mus.) proved on examination to be *G. tournieri*, but the data relating thereto amounts only to the supposed place of capture, Lichfield, Staffs. The species cannot be fully accepted to the British list.

G. tournieri is found over the whole of Europe.

Biology.—Of the life-history and hosts of the species nothing is recorded. The imagines, as in other species of *Gasteruption*, emerge in mid-summer, and visit Umbelliferous flowers and Compositas, including *Daucus carota* L., *Heracleum sphondylium* L., *Anthriscus cerefolium* (L.), *Achillea millefolium* L. and *Solidago canadensis* L.

[(5) *Gasteruption rubricans* (Guérin, 1828).]

G. esenbeckii (Westwood, 1841), *G. dorsalis* (Westwood, 1841).

Length.—9½–11 mm.

Head black in male, red in female, but commonly dark behind ocelli; mandibles red; sculpture of head coarsely shagreened to finely granulate; reflexed collar absent but head narrowly bordered; malar area short; distance from eye to posterior ocellus equal to the distance between posterior ocelli. Scape of antenna red, flagellum dark; 3rd antennal segment one and a half times as long as 2nd, and equal in length to 1st; fourth in male shorter than 3rd, in female equal to it.

Thorax black in male, red in female, except for ventral side, scutellum and variable area of prescutum and scutum which are dark; mesonotum granulate, often more strongly rugosely punctured in the male. Legs red, coxae, and sometimes femora, darker.

Abdomen rufous, with paler red marks on the 2nd–4th segments. Ovipositor short, equal in length to first two abdominal segments together; valves dark.

The female of *G. rubricans* cannot be confused with any other British species, while the male is quite separable by the red legs and mandibles and the mesonotal sculpture.

Distribution.—The claim of this species to any place in the British list depends upon a single female reputedly taken at Lichfield, Staffs (Carr). As in the case of *G. tournieri* in the same collection (Oxf. Mus.) the data are very incomplete. Carr himself seems to have regarded the specimen as an erythristic variety of *G. assectator*.

Abroad *G. rubricans* enjoys a very wide range, being found from S. Sweden, across the whole of Europe, to North Africa, and east to Asia Minor and Palestine; it is not surprising, therefore, that it should be found at some time in England, especially as the genera it is known to parasitize occur here.

Biology.—Adults are found on plants, including *Daucus carota* L., *Anthriscus cerefolium* (L.), *Pimpinella saxifraga* L., and a male once on *Calluna vulgaris* (L.). The larvae are parasites of a number of Hymenoptera, including *Odynerus laevigata* Schuck., *Osmia tridentata*, and according to Höppner (1904) *Prosopis variegata* in the stems of *Rubus*.

(6) *Gasteruption minutum* (Tournier, 1877).

G. longigena Thomson, 1883.

Length.—8-9 mm.

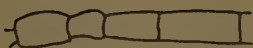
Head black, shagreened, with a very narrow black margin, strongly curved, but no reflexed collar; malar area large, equal in length to width of mandible at base, or to first antennal segment (fig. 2), this character alone serving to distinguish this species from others



14



15



16



17



18



19

FIGS. 14-19.—*Gasteruption*. Basal segments of male antennae. (14) *G. jaculator*; (15) *G. pedemontanum*; (16) *G. assectator*; (17) *G. minutum*; (18) *G. minutum*; hind tibia, dorsal; (19) *G. assectator*, hind tibia.

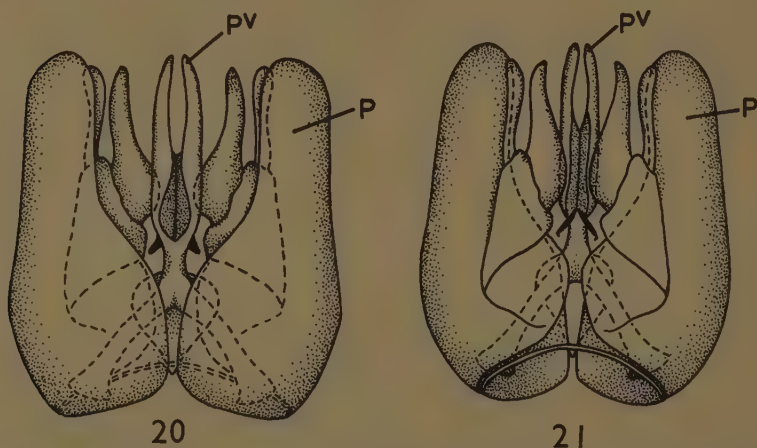
of the genus in Britain. Distance between eye and posterior ocellus almost as great as that between posterior ocelli. Male antennae with 3rd segment equal in length to 1st, 4th equal to 2nd and 3rd together (fig. 17).

Thorax dull black; punctures of pronotum shallow and sub-circular; propleuron almost smooth; mesonotum shagreened, more strongly in male than female; propodeum finely wrinkled. Coxae finely shagreened, except hind coxae of male, which are finely transversely striated; fore and middle tibiae red at base; underside of hind tibiae red for basal third; hind tarsi dark. Posterior tibiae longer and narrower at the base than in *G.*

assectator (fig. 18). Abdomen with red marks at junctions of tergites 2-6 in male and 2-5 in female, the last mark being smaller than the others, and underside of segment 2 rufous. Parameres of genitalia strongly rounded laterally, aedeagus with free apices of penis-valves short (fig. 28). Penis-valves evenly convex laterally; proximal tooth of latter small (*ptv*, fig. 30); basal aedeagal plate (*ap*, fig. 28) acuminate anteriorly. Ovipositor in female very short, only as long as first abdominal segment; valves entirely dark.

G. minutum is distinguishable from *G. assectator*, the only closely similar species, by the large malar area, the more strongly shagreened head and less strongly shagreened mesonotum, the shorter ovipositor in female, smaller extent of red on abdomen, and smaller size.

Distribution.—This species was first recorded from Britain by Capron (1880), who took a female in Surrey. Since that date it has been taken in the following localities: Mill Hill, Middlesex; Slough, Bucks; West Gloucester; Croyde, North Devon; and West Cornwall.



FIGS. 20-21.—*Gasteruption jaculator*. Male genitalia, dorsal and ventral. *p*, paramere; *pv*, penis-valve.

The Continental range is very imperfectly known, largely owing to former confusion with *G. assectator*; it has, however, been reliably identified from Scandinavia, Switzerland, France and the Channel Islands.

Biology.—The paucity of information concerning the habits and life-history of the British species of *Gasteruption* is nowhere so marked as in *G. minutum*. As the other species imagines occur from June to August, and one has been captured on the Cow Thistle (*Sonchus arvensis* L.).

(7) *Gasteruption assectator* (Linnaeus, 1758).

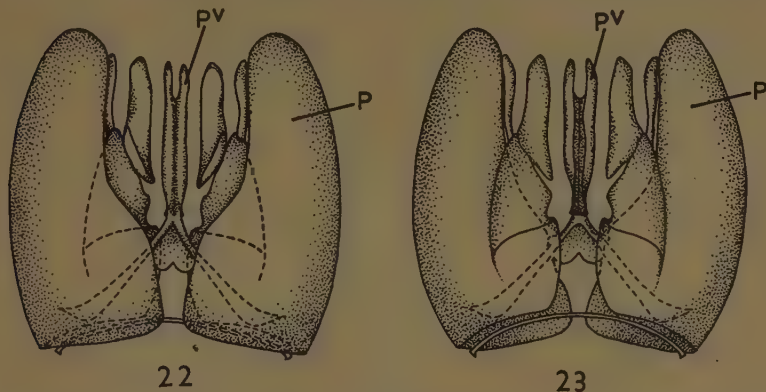
G. assectator auctt.

Length.—8-12, usually 10 mm.

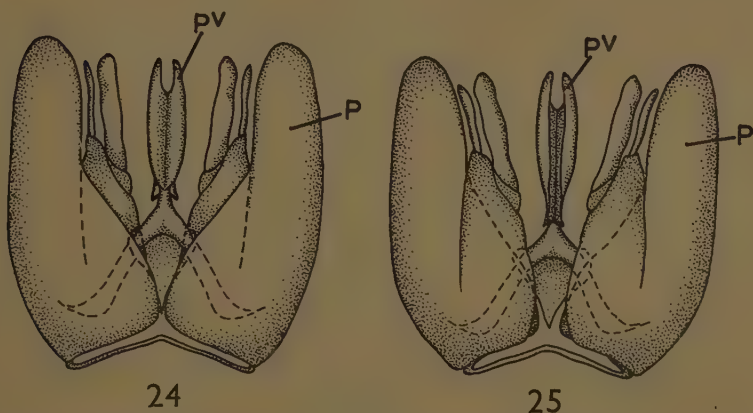
Head black, shagreened, hind-margin almost straight, with a narrow black occipital ridge, but not a reflexed collar; malar area very short; distance between posterior ocelli a little greater than that between posterior ocellus and eye; eyes sometimes glabrous, but

commonly clothed with short sparse pubescence, particularly towards the posterior margin. Male antennae with 3rd segment one and a half times as long as 2nd, 4th nearly as long as 2nd and 3rd together; in female 4th segment is twice as long as 2nd.

Thorax black; pronotal punctures sub-circular, and deep; processes very small; propleuron almost smooth; mesonotum shagreened, very strongly in male; mesopleura



FIGS. 22-23.—*Gasteruption assectator*. Male genitalia, dorsal and ventral. *p*, paramere; *pv*, penis-valve.

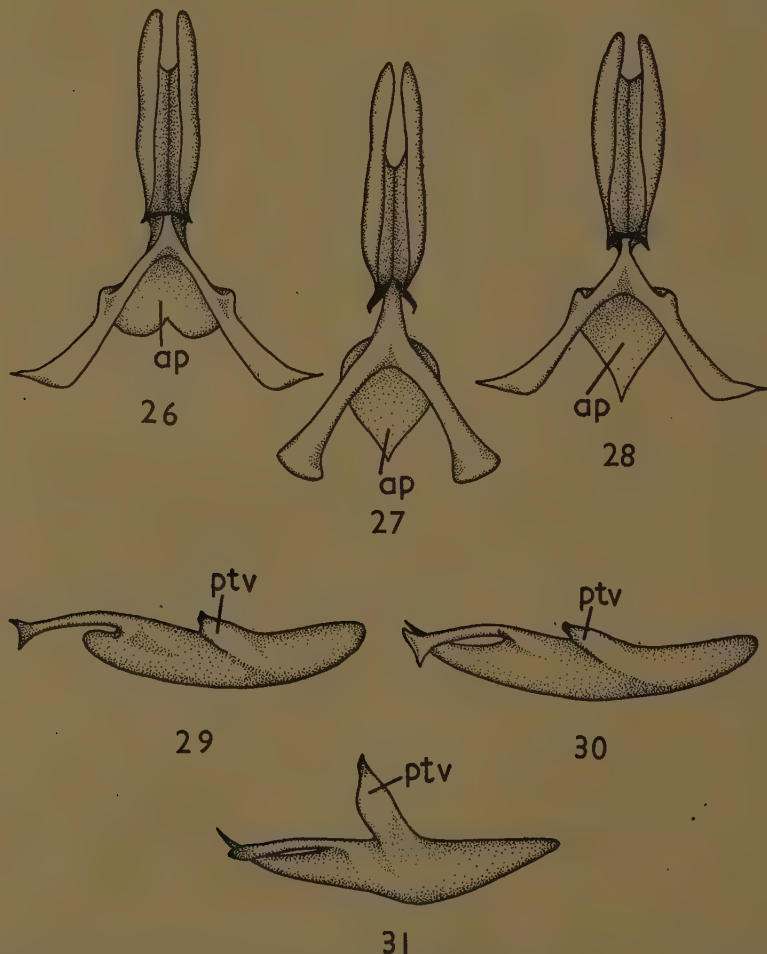


FIGS. 24-25.—*Gasteruption minutum*. Male genitalia, dorsal and ventral. *p*, paramere; *pv*, penis-valve.

with reticulate wrinkling in male; propodeum strongly wrinkled in male, coarsely shagreened to finely reticulate in female. Coxae finely shagreened, except for hind coxae of male, which are transversely striated dorso-laterally. Front and middle tibiae and tarsi, underside and basal ring of hind tibiae, and hind tarsi of male red. Female with all tibiae and tarsi black, except for yellow mark on underside of hind tibiae towards the base. Hind tibiae shorter and broader at the base than in *G. minutum*. Abdomen black; male with 4,

female with 3, orange-red marks on each side; in the latter sex nearly the whole of tergites 3 and 4 are red. Male genitalia with parameres evenly rounded laterally; free apices of penis-valves short (fig. 26), side-margins of valves slightly sinuate, and not evenly convex as in *G. minutum*: proximal tooth of penis-valves (*ptv*, fig. 29) short; basal aedeagal plate (*ap*, fig. 26) bilobed anteriorly. Ovipositor of female shorter than abdomen, one and a half times as long as first abdominal segment; valves black.

Although *G. assectator* closely resembles *G. minutum*, it differs in the larger size, much shorter malar area, less strongly shagreened head and more strongly



FIGS. 26-31.—Ventral and lateral views of aedeagus of *Gasteruption*. (26) and (29) *G. assectator*; (27) and (31) *G. jaculator*; (28) and (30) *G. minutum*. *ptv*, proximal tooth of penis-valves; *ap*, basal aedeagal plate.

shagreened mesonotum, larger extent of red on abdomen, and longer ovipositor in female. Well-marked differences exist in the male genitalia, particularly in the shape of penis-valves and basal aedeagal plate.

Distribution.—*G. assectator* is one of the commonest British Evanioids, good records existing from Surrey (Ingall, 1895), North and South Essex (Nicholson, 1928), East and West Kent, Bucks, Oxford, Cambridge, East and West Suffolk (Morley, 1937), Norfolk, South Hants, South Devon, Padstow (Cornwall), Staffs, and Glamorgan. Stelfox (1929) records the species from Co. Wicklow, Eire. Outside the British Isles *G. assectator* occurs over the whole of Europe from Lapland to Sicily and eastwards to Asia Minor; also N. E. United States.

Biology.—Much more is known of the biology of this species than of any other species of *Gasteruption*; Hoppner (1904) has provided an account of the life-history of *G. assectator* which probably typifies the genus as a whole. The eggs are attenuated and pedunculate, with the stalk not thickened at the free end. An egg is laid on the surface of the body of a mature larva of *Prosopis*, either before or after closure of the cell. The *Gasteruption* larva which emerges is 14-segmented, and possesses nine pairs of spiracles, situated on the 3rd and the 5th–12th segments. When fully mature the larva is elongate, measuring 7–7½ mm. in length and 2–2¼ mm. in breadth, the mandibles are tridentate, and the body is clothed with bands of stout, brown, backwardly-directed chaetae, most evident on the dorsal side.

After consuming the first host-larva the *Gasteruption*-larva bites its way into a neighbouring cell and devours a second *Prosopis* larva before reaching maturity; at pupation a cocoon is formed within the cell of the host, and the imagines emerge in June. These may be found from June to August, visiting flowers of UMBELLIFERAE such as *Anthriscus sylvestris* (L.), *A. cerefolium* (L.), *Heracleum sphondylium* L., *Daucus carota* L., *Pimpinella major* (L.), *P. saxifraga* L., *Pastinaca sativa* L. and *Angelica sylvestris* L., and also *Euonymus* and *Rhododendron*. It has also been taken on timber in Co. Wicklow.

G. assectator is remarkably unspecific in its choice of host, Hoppner recording it as parasitic within cells of various species of *Prosopis* in the stems of *Rubus*; these include *P. annularis* (Kirby), *P. pectoralis* (Foerster), *P. brevicornis* (Nylander), *P. communis* (Nylander); according to the same author it is also a parasite of the Sphecid wasp *Trypoxylon figulus* (L.). Whether these species are parasitized in the British Isles as well as on the Continent is unknown, but *G. assectator* has been bred from a tree-stump containing a nest of *Chelostoma florissomme* (L.) (vide Nicholson, 1928).

Appendix to *Gasteruption assectator*.—The names of two species of *Gasteruption* other than those which have been described have appeared in British lists, viz., *G. abeillei* Kieffer, 1912, and *G. rugulosum* (Abeille de Perrin, 1879). Examination of the specimens from which these records were made shows that in both cases they are of *G. assectator*.

G. abeillei: Two specimens (B. M. Coll.) originally thus named were taken by Nixon at Otford, Kent, and listed under this name by Waterston (1928) and Kloet and Hincks (1945). Perkins and the writer conclude from their examination that the specimens are in fact of *G. assectator*.

G. rugulosum: A male and female *Gasteruption* bred from *Prosopis pectoralis* (*kriechbaumeri*) at Wicken Fen by Spooner in 1929 (now in Cambs.Mus.) were identified by Ferrière as *G. rugulosum*, this name appearing in the check-list of

Kloet and Hincks. Ferrière subsequently examined a number of types of *Gasteruption* and found that *G. rugulosum* was synonymous with *G. freyi* (Tournier, 1877) which he describes in his paper on the Swiss species (1946) as possessing a reflexed collar. The specimens in question have no reflexed collar, and further agree with *G. assectator* in the shape of the head, the pubescence of the eyes, relative lengths of the antennal segments, sculpture of the thorax, the red front and middle tibiae and tarsi of male, extent of red on abdomen, and the length of the ovipositor in the female. The writer therefore has no hesitation in regarding the two specimens as being of *Gasteruption assectator*.

7. A CHECK-LIST OF THE BRITISH EVANIOIDEA.

Family: AULACIDAE.

Aulacus Jurine, 1807.
striatus Jurine, 1807.
arcticus Dahlbom, 1837.
exaratus Giraud, 1850.

granulithorax (Tournier, 1877).
obliteratum (Abeille de Perrin, 1879).
thomsoni Schletterer, 1885.

Family: EVANIIDAE.

Evania Fabricius, 1775.
appendigaster (Linnaeus, 1758).
laevigata Olivier, 1791.
fuscipes Illiger, 1807.
Brachygaster Leach, 1830.
minutus (Olivier, 1791).
fulvipes (Curtis, 1829).

foveolum Szépligeti, 1903.
pedemontanum (Tournier, 1877).
terrestre (Tournier, 1877).
minutum (Tournier, 1877).
longigena Thomson, 1883
assectator (Linnaeus, 1758).
affectator auctt.
 ?? *tournieri* Schletterer, 1885.
jaculator (Tournier, 1877).
 ?? *rubricans* (Guérin, 1828).
esenbeckii (Westwood, 1841).
dorsalis (Westwood, 1841).

Family: GASTERUPTIONIDAE.

Gasteruption Latreille, 1796
Foenus Fabricius, 1798.
jaculator (Linnaeus, 1758).

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Journal of the Entomological Society of the South of England.

Transactions of the Entomological Society of London; continued as the *Transactions of the Royal Entomological Society of London*.

The Essex Naturalist.

Transactions of the North Staffordshire Field Club.

Transactions of the Suffolk Naturalists' Society.

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INSOLATION AND ANT POPULATION IN THE WEST OF SCOTLAND.

By M. V. BRIAN and A. D. BRIAN.
(Department of Zoology, Glasgow University.)

Manuscript received 8th October, 1950.

(Read 6th June, 1951.)

With 1 Text-figure.

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1. INTRODUCTION.

THIS study was made in the West of Scotland, in Dunbartonshire on the north side of the Firth of Clyde. The area as a whole has a south-westerly aspect, and rises more or less gradually from sea-level to a height of nearly 1000 feet in one-and-a-half miles. It is thus exposed to the prevailing winds and frequent heavy rain as well as the occasional sunshine. This "oceanic" climate, of cool wet summers provides an excuse for further adding to the long list of European ant surveys, for all these have come from areas with drier, and most from areas with warmer summer climates. But in addition to survey, an effort has been made to analyse the relevant factors in distribution, and discover their method of action. In this paper, this last aspect is approached first; mainly through a comparative study of *Myrmica rubra* L. (= *M. ruginodis* Nylander) in various habitats, and by laboratory and field experiments. Survey results are confined to the changes in two man-initiated subseres—that following heather burning and that following the felling of woodland. The biotic plagio-climaxes into which these may turn under the influence of grazing and browsing are more complex and enduring, and their treatment will be deferred until a later paper.

The ant fauna is comparatively poor. Donisthorpe (1927) mentions only 19 species in 7 genera for Scotland, and of these, only eight, of four genera, *Formica*, *Lasius*, *Myrmica* and *Leptothorax*, are at all frequent. In the locality studied only four species were common: *Formica fusca* L., *Myrmica scabrinodis* Nylander, *M. rubra* L. and *Leptothorax acervorum* F. In addition, two colonies of *Myrmica lobicornis* Nylander and one colony of *M. sulcinodis* Nylander have

been discovered. It is also possible to say that certain ants, locally common elsewhere in Scotland, are absent: these are *Myrmica laevinodis* Nylander, *Lasius flavus* F., *L. niger* L. and *Formica rufa* L.—a fact of which an explanation would be very desirable. This fauna contrasts strikingly with that of central Germany, where Gösswald (1932) mentioned fifty species and varieties of eighteen genera. It is as poor as that of East Karelia with a cooler but much drier summer where Hölldobler (1944) recorded seven species in virgin woodland.

The soil is derived from a coarse red sandstone (Devonian) for the most part, but in a few places from a stickier glacial drift. Being sandy and porous and usually on a good slope, it drains easily, and may sometimes become quite dry. Agricultural land extends from the coast up to about 300 feet, and is followed by moorland of varying intensity: sometimes pure Callunetum with grouse (*Lagopus scoticus*), and sometimes, principally at lower levels, near the Agricultural zone, *Calluna vulgaris* L., and *Erica cinerea* L. interspersed with *Festuca-Agrostis* grassland. The extent and character of this marginal belt, grazed by sheep, hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) has varied in the past 100 years or more with fluctuations in agricultural activity. Woodland in this district consists of either mixed deciduous trees of considerable age or recent plantations of conifers. A great deal of the former type felled during the past 30 years has been left untouched, and is in various stages of regeneration or biotic plagioclimax.

2. *Myrmica rubra* IN OPEN AND SHADED HABITATS.

Myrmica rubra is the most abundant and eurytopic of the 4 common species, occurring as the form *macrogyna* (Brian and Brian, 1949) in open habitats with the other three, and extending alone into the shadier parts of woodland.¹ A comparison has been made in various ways of the populations in the two habitat types.

In the first place, nests were sampled in mid-July and the degree of maturation of the brood established. Samples representing the two habitat types were taken from various localities, and in each case the entire brood of a colony was examined to avoid errors due to non-random assortment of brood in the nest. After a classification into ontogenetic stages, the pupae were subdivided according to their degree of pigmentation. Whilst their body remains white, the eyes change from brown to black; and later, the whole body gradually changes to brown. Clearly, no sharp distinctions could be drawn, nor is it intended to imply that the times normally spent in each category are equal, but the classification was very useful. In the exposed nests, brood from eggs laid the same year had in some cases just reached the third instar (and thus could not be distinguished with certainty from the hibernated brood). Accordingly, in these cases all larvae were ignored, but it is thought, from breeding experience, that all the hibernated brood had metamorphosed, and a small part of the current season's brood may have done so as well. In the shaded nests the current brood remained in the egg and early larval stages and could easily be distinguished. A few new adult workers may have emerged in the exposed nests, but no attempt was made to distinguish them from the older workers.

¹ Throughout this paper the only form of *M. rubra* encountered is *macrogyna*.

Considerable differences existed (Tables I and II). In the shaded nests,

- (1) the brood was much retarded (and the state in exposed nests only reached a month later);
- (2) there was less brood (and this implies that the colonies were smaller;
- (3) they were failing to reproduce (the residual larvae in these nests yielded workers).

TABLE I.—*Myrmica rubra*: Brood Condition in Mid-July, 1946, in Exposed Nests.

Sample number.	Sex and caste.	Prepupae.	Pupae				New adults (except workers).	Total.
			Eyes white.	Eyes brown.	Eyes black.	Body brown.		
1	Workers	38	144	256	228	21	.	1354
	Males	.	0	0	34	256	0	
	Females	.	0	0	0	248	129	
2	Workers	125	156	226	81	10	.	1303
	Males	.	0	0	0	257	0	
	Females	.	0	0	0	448	0	
3	Workers	0	36	269	63	5	.	1262
	Males	.	0	0	166	5	0	
	Females	.	0	0	0	510	208	
4	Workers	92	122	268	168	61	.	1084
	Males	.	0	0	0	354	0	
	Females	.	0	0	0	19	0	
5	Workers	164	85	172	262	73	.	854
	Males	.	0	10	0	0	0	
	Females	.	0	0	88	0	0	
6	Workers	84	123	144	148	89	.	755
	Males	.	0	0	3	164	0	
	Females	.	0	0	0	0	0	
7	Workers	148	79	88	25	0	.	732
	Males	.	0	0	244	148	0	
	Females	.	0	0	0	0	0	
8	Workers	119	119	119	63	210	.	691
	Males	.	0	0	0	60	1	
	Females	.	0	0	0	0	0	
9	Workers	118	91	141	119	1	.	553
	Males	.	1	3	79	0	0	
	Females	.	0	0	0	0	0	
10	Workers	0	2	6	3	2	.	13
	Males	.	0	0	0	0	0	
	Females	.	0	0	0	0	0	

Caste and sex of prepupae indistinguishable.
 Third instar larvae neglected, but probably few.
 Females = winged females.

In fact the ant colony, considered as an organism, showed striking resemblance to several plants under similar circumstances ; for example *Rubus fruticosus* L., the blackberry, and *Pteridium aquilinum* (L.) Kuhn, both of which exist, but do not flourish in shady habitats.

TABLE II.—*Myrmica rubra* : Brood Condition in Mid-July in Shaded Woodland Nests.

Sample number.	Sex and caste.	Hibernated larvae.	Prepupae.	Pupae.	Total.
1	Workers	99	224	71	394
	Males	0	0	0	
2	Workers	32	145	114	336
	Males	0	0	45	
3	Workers	27	134	84	245
	Males	0	0	0	
4	Workers	51	36	6	93
	Males	0	0	0	
5	Workers	42	36	2	80
	Males	0	0	0	
6	Workers	42	25	0	67
	Males	0	0	0	
7	Workers	34	23	2	59
	Males	0	0	0	
8	Workers	45	14	0	59
	Males	0	0	0	
9	Workers	25	7	0	32
	Males	0	0	0	
10	Workers	8	10	0	18
	Males	0	0	0	

All pupae were in the " eyes-white " stage ; none more mature.

No winged female brood was present.

No new adults of any sex or caste were present.

Before considering these results in more detail, it is convenient to present a few further differences which have been discovered. These concern the size of the workers. It was thought after casual inspection that workers were smaller in shaded nests. But workers are larger in large colonies, and since, as has just been indicated, colonies in woodland are smaller than colonies outside (on the average), the possibility that the dwarf size of woodland workers might be accounted for solely by differences in colony-size had to be considered. The difficulty was resolved by the use of analysis of covariance methods. The size of workers in a colony was arrived at by taking the average of the head-widths of as many as possible (up to 25) ; and, in each colony, the total number of workers was counted. The relation between these two factors, " average-head-width-of-worker " and " colony-size," was curvilinear (fig. 1), but easily rectified by using the common logarithm of the numbers of workers. When this was done it was found that linear regression within

the two habitat types was good ($P < 0.1$ per cent.) and the regression lines gave no indication of differing in slope ($P > 10$ per cent.), but the woodland line lay well below the exposed line (the difference between adjusted habitat head-width means had a probability by chance of less than 0.1 per cent.). This indicated that, for a given colony-size, the workers outside were larger than those inside the woodland.² If these curves are accepted at face value, another item of interest emerges: that they diverge from a common point having a colony-size of 10 workers, thus implying that the environmental differences do not begin to have effect until this colony-size is exceeded.

The samples from woodland were taken without deliberate bias, and can be regarded as indicating the size of colony existing there. They range from

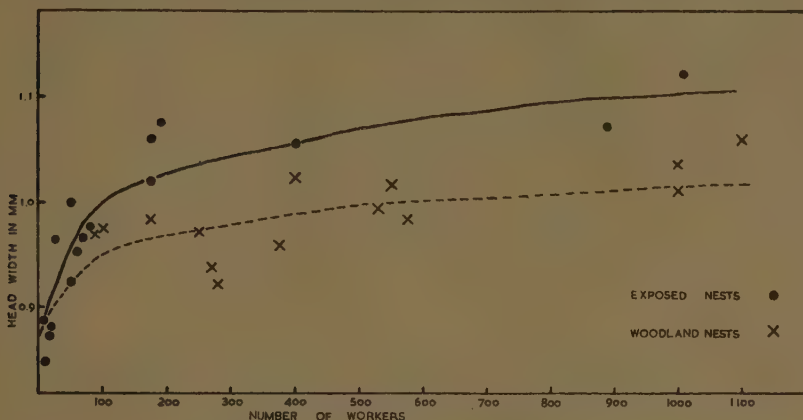


FIG. 1.—The relation between the numbers of workers in a colony (x) and their average head-width (y) in two types of habitat; fully insolation exposed (full line) and pine plantation (broken line). The actual points are given and the best fitting lines. These have the equations:

$$y = 0.113 \log x + 0.766 \text{ (exposed), and } y = 0.072 \log x + 0.810 \text{ (woodland).}$$

76 to 1514 workers, that is, up to about half the known maximum size of nests in open habitats. This was given as about 3000 by Brian (1950).

Intraspecies habitat differences in worker-size have been shown to exist in the ant *Cardiocondyla strambulowi* by Arnoldi (1926). Ants living in dry vegetation-bound sand were smaller than those in dry salt-marsh populated by *Plantago maritima* L. and other halophytes. This difference could perhaps be attributed to food-supply.

It has even been possible to extend this line of investigation a little further, and include numerous degrees of exposure to sunlight instead of a simple contrast between two levels. This was done in a plantation of pines (*Pinus sylvestris* L.) 14 years old and 8 to 10 yards high. Apart from the two previous measurements, a third, "potential hours sunlight," was included and calculated (to the nearest half-hour) from the size of the gap between trees at the level of

² The actual mean size of worker for woodland nests was greater than for exposed nests, but this was because many small nests were deliberately included in those collected from the exposed situations. Adjustment for colony-size reversed and at the same time increased the difference.

the sun's transit (in May). It was, of course, the "potential" as distinct from the "actual" amount of sunlight received—as no account was taken of the effect of cloud screening.

The logarithm of colony-size (z), and the average worker head-width (x), were both positively correlated with the potential insolation (y): $r_{yz} = 0.611$, 1.5 per cent. P ; $r_{xy} = 0.852$, <1 per cent. P . As in the previous samples, average head-width was positively correlated with log colony-size: $r_{xz} = 0.594$, 1.5 per cent. P . The reduction in variance of head-width due to multiple regression with the other two factors was significant ($P < 1$ per cent.) with a multiple regression coefficient R , equal to 0.857. The standard regression equation,

$$x = \beta_{zy.z} y + \beta_{xz.y} z, \text{ was as follows,}$$

$x = 0.78y + 0.12z$, thus indicating that, in these samples, the greater part of the variation in head-width was associated with variation in potential insolation (y) rather than with variation in colony-size. In fact, only the first of these two standard partial regression coefficients is significantly greater than zero. This is to say that, as in the previous investigation, with only two levels of insolation, the degree of exposure has a direct and positive influence on the size of the workers, independently of colony-size. As exposure increases, so does worker head-width and general body-size.

The further significance of this multiple regression will be dealt with in the discussion, after experimental data and field survey data have been presented.

3. SUNLIGHT AND TEMPERATURE.

Before describing the results of an experimental investigation into the observations just recorded, it is desirable to know the extent to which sunlight reaches the soil under various vegetations, its effect on the temperature of the soil, and, finally, the effect of this temperature on ant growth.

TABLE III.—*The Percentage Penetration of Direct Sunlight to Soil Surfaces under Various Vegetations.*

Vegetation.	Mean penetration.	Standard deviation.
Larch plantation 14 years old	25±4.5	25
Pine plantation 14 years old	23±5.3	29
Oak wood	20±4.3	24
Beech wood	7±0.7	4
Meadow grass 1 foot tall	1±0.3	0.7
Bracken	0.6±0.1	0.5

Sunlight penetration was measured with a photometer, perpendicular to the rays, moved randomly into a series of positions at various stations on the soil of the area investigated. All observations were made on cloudless days, and the light penetration expressed as a percentage of that from the unscreened sun. This data is presented in Table III. These figures express what is familiar (in the case of woodlands) as a subjective impression. The larch and pine plantations let a good deal of light through and formed a very heterogeneous pattern on the floor—giving a high variance to the readings. This micro-heterogeneity is, of course, no use to the ants—they cannot select a

sunlight spot to live in—for the whole pattern is continually moving. Bracken and grass cut out much more light than any of the woodland types, although beech comes near to them in this respect. The light intensity beneath these last two herbaceous types on a bright sunny day is about the same as in the open on a dull cloudy day.

Sunlight reaching the soil surface causes a very appreciable rise in temperature, which is largely affected by the type of surface and the ease of conduction into the deeper soil layers. Stones, if not more than an inch or two thick, trap heat not only because they absorb radiation very effectively, but because they tend to develop an air space below them which reduces conduction to the substratum. This air space may be caused by a variety of animals consuming the compressed and dying vegetation, but is, in sunny places, often due to ants. There is no doubt that they move their brood up and down in galleries under stones in response to changes of temperature—as Steiner (1929) has shown. For *Myrmica rubra* he found that when temperatures of 29–31° C. were reached

TABLE IV.—*Temperature Regimes under a Slate and in Shade during Intermittent Sunlight.*

Under slate.	In shade.
17.5	15.5
21.5	15.5
26.0	15.5
29.0	15.5
24.0	15.0
21.0	14.5
19.0	15.0
23.0	14.5
24.5	14.0
28.5	13.5
30.0	14.0
25.5	14.0
26.5	14.5
28.5	14.5
29.0	14.5
28.0	14.5
28.0	14.0
Mean	25.3
Range	12.5
	14.6
	2.0

Recordings at 15-minute intervals. Temperature in shade was taken on the soil surface under 2 inches of grass, in degrees Centigrade.

at the surface, the ants moved away; full brood was up at a temperature of 24–25° C. These results apply well to the same species in our locality.

The temperature under these sun-exposed stones is considerably higher than air temperature or soil surface temperature under 2–3 inches of grass in shade even on half cloudy days, as the data in Table IV show. During periods of insolation the slate temperature rose, but never had time to reach its maximum (in the order of 40–45° C.) before the arrival of cloud caused a fall. In

spite of considerable fluctuation, however, the slate temperature always remained above that of the grass in shade. It will be shown later that the additional 10° C. which it maintained lies in a range which confers a very significant advantage on *Myrmica rubra*.

The sum of a temperature régime and at the same time its relevance to ants, is easily assessed in the various microclimates by placing artificial nests in the places of interest. Probably the simplest case, technically, is a comparison of the ontogenetic rates of non-feeding brood. Prepupae were placed in glass tubes with a moist cotton-wool pad and a cotton-wool plug; a few attendant workers were included. The whole was wrapped in wire gauze to prevent the interference of small mammals and placed on the soil surface under various vegetations. The simplicity and uniformity of these cultures make them nearly ideal measures of relevant temperature régimes.

TABLE V.—*Myrmica rubra*: Temperature Relevance to Ontogeny in Various Vegetationally Produced Microclimates and at Two Laboratory Constant Temperatures.

Group.	Microclimate:		Under grass 2-3 in.	Under grass 10-12 in.	Under dense bracken, larch wood and pine wood.
	25° C.	18° C.			
A	All adult by day 12	All adult by day 23	Bodies brown	White bodies, black eyes (a trace of brown in body)	White bodies, black eyes
B	All adult by day 17	All adult by day 35	Brown pupae	Pupae with white bodies, black eyes	All failed in transition to pupae and died.

A = Initially new worker pupae; results shown after 26 days.

B = Initially prepupae; results shown after 41 days.

The pine wood was the same as the plantation referred to in the statistical study of gap-size in relation to ants; trees of *Pinus sylvestris* 14 years old.

Seven systems were compared (Table V); two were constant laboratory temperatures, and five were soil surfaces under various plant covers. The floors of dense bracken, larch wood and pine wood (shaded places, not glades) were the coolest; so cool that the prepupae were unable to cast their larval skin and enter the pupal stage. This alone is a sufficient reason for the absence of ants in such places. The floor under tall meadow grass was not quite as cool; in fact it was warm enough for pupation to take place successfully, and maturation was slightly quicker. Under short grass progress was rapid, but not quite as rapid as at either constant temperature. The lower of these, 18° C., is only a few degrees above the metamorphosis threshold, but its continuous persistence gave it more effect than the fluctuating grass temperatures. The higher constant temperature, 25° C., is the preferred temperature under stones (as has already been mentioned) and it also lies near the optimum for brood development; higher temperatures cause more mortality.

These results indicate clearly that the differences in brood maturation in nests from shaded and exposed situations presented in the first part of section 3 could be entirely explained by temperature differences in the microclimates.

In grassland the two *Myrmica* species build mounds, rarely more than 6 inches high and as broad, which enable them to reach the sunlight. These are not as effective in heat-capture as slates, for in an area of grassland where slates had been put down for experimental purposes a comparison of brood maturity was made. It was found that, under slates by the end of May, the majority of the brood had defecated, whereas in mound nests (and nests under logs) it had only just stopped feeding. This difference—about 3 days at 25° C.—is significant, although small compared with the difference between fully exposed and shaded woodland nests.

In warmer, less cloudy climates, no doubt the importance of direct access to solar radiation, is much diminished. In this locality, however, during the 5 summer months, April to September, of 1947 and 1948, the maximum air shade temperature was below 15° C. on 26 per cent. of days, and the minimum never rose above 15° C.—roughly the threshold of metamorphosis in *Myrmica rubra*. On only 11 occasions in 1947 and 7 in 1948 did the air shade temperature exceed the optimum and "preferred" temperature, 25° C.³

4. EXPERIMENTAL ANALYSIS.

So far, the differences between the ants in shaded and exposed nests of *Myrmica rubra* have been shown to concern—

- (a) the degree of maturation of brood,
- (b) the size of workers, and
- (c) the size and maturity (i.e., the ability to produce sexuals) of colonies.

Considerable temperature differences have been shown to exist in the nesting zone, due to differing degrees of insolation, and these proved to be ant-significant affecting ontogeny rate, and sometimes survival. Whilst the latter is certainly an element in determining colony-size, no evidence has so far been obtained of the effect of temperature on the second variable, worker-size. It is here that another environmental factor, food-supply, would seem most likely to be involved; and it might also interact with the observed effects of temperature on the two other variables. Moreover, food-supply is indirectly dependent on insolation, for much ant food is obtained from aphids living on herbs whose existence in woodland is much affected by the extent to which light penetrates the trees. This section describes experiments designed to elucidate these points.

The experiment on prepupal maturation was first of all repeated at two constant temperatures, 15° C. and 23° C., to determine the influence of temperature on survival and adult-size, as well as on the rate of ontogeny. Three colonies of each of the two species, *Myrmica rubra* and *M. scabrinodis*, were used, and the prepupae from each colony were divided equally between each temperature. Both treatments thus had three replicates, each from a different colony. The species gave no sign of differences in rate of maturation at either temperature. Survival was lower at the lower temperature; for *rubra* it fell from 64 per cent. to 35 per cent., and for *scabrinodis* from 77 per cent. to 38 per cent. (combining replicates.) No differences in size due to temperature treatment were detectable by analysis of variance.

This is not surprising, for the size of the adult is subject to little alteration after defecation. The start of experimental culture was therefore moved back

³ Meteorological data kindly supplied by the Burgh Surveyor, Helensburgh.

to another convenient point in ontogeny—the post-dormant hibernated final-instar larva. At this stage the individual is about half grown, and it had earlier been established that they were susceptible to experimental modification. From a single colony of *Myrmica rubra* 250 of these were chosen, all of small size (to avoid males and winged females in the progeny). Five groups of 50 were formed and each was cultured at 15° C. for a period before being transferred to 23° C. The durations at the lower temperature were 0, 2, 3, 6 weeks and all the time, for the 5 cultures respectively. At transfer the larvae which had not metamorphosed were measured—and this was the majority (Table VI).

TABLE VI.—*Myrmica rubra* : Culture of Hibernated Larvae for Varying Periods at 15° C. before Raising to 23° C. Length of Larvae at Transfer.

Length of larvae at transfer.	Period at 15° C. (weeks).			
	0.	2.	3	6
10	6	.	.	.
11	11	.	.	.
12	17	1	.	.
13	9	.	.	.
14	3	.	.	.
15	4	3	2	1
16	.	3	.	.
17	.	1	1	.
18	.	1	1	.
19	.	3	2	.
20	.	4	.	3
21	.	4	.	2
22	.	3	1	3
23	.	3	1	2
24	.	2	1	2
25	.	.	2	.
26	.	3	1	1
27	.	4	1	5
28	.	4	3	4
29	.	2	4	2
30	.	3	2	1
31	.	1	3	2
32	.	3	6	4
33	.	2	4	4
34	.	.	4	4
35	.	.	5	1
36	.	.	2	1
37	.	.	1	.
38	.	.	1	.
39	.	.	1	.
Total larvae	50	50	49	42
Other brood	—	—	—	{ 1 prepupa 1 pupa

Length in micrometer divisions : 10 div. = 1 mm. approx.

This showed that growth was possible at 15° C., but only a little metamorphosis. But one new factor emerged : that prolonged exposure to the lower temperature caused a return to dormancy. Thus the culture with 6 weeks at 15° C. which had 2 individuals in process of metamorphosis at transfer only added 8 more at the higher temperature ; 20 surviving larvae remained quiescent. Due to a combination of return to dormancy, and mortality, the actual adult production was inversely proportional to the time at 15° C. (Table VII).

TABLE VII.—*Myrmica rubra* : Culture of Hibernated Larvae for Varying Periods at 15° C. before Raising to 23° C. Frequency-distributions of Head-widths of Emerging Workers.

Head width.	Period at 15° C. (weeks).				All time.
	0.	2.	3.	6.	
29	.	.	1	.	.
30	.	.	1	.	.
31	.	.	4	.	.
32	.	.	3	.	.
33	5	1	1	.	2
34	12	5	3	1	3
35	11	7	1	1	1
36	7	7	—	2	.
37	1	4	1	5	.
38	.	.	.	—	.
39	.	.	.	—	.
40	.	.	.	1	.
Total	36	24	15	10	6

Head-widths in micrometer divisions : 1 div. = 0.0303 mm.

Examination of the sizes of the adult progeny yielded an interesting result. No differences could be detected between adults nurtured constantly at either temperature, but if raised in a certain stage of growth they became unusually small. These dwarfs are seen only in the culture exposed for three weeks at 15° C. ; they were the first adults to emerge, and were derived from amongst the larvae that were 35 or more units long at transfer—a size of which this culture had ample. Further investigations, which need not be detailed here, have shown that larvae pass into a stage at this size which commits them to metamorphosis, but does not prevent assimilation. Provided temperature remains steady, considerable growth may occur, but a rise hastens metamorphosis without a proportionate, and compensating, increase in assimilation.

There is thus, from this experiment, confirmation of the brood-retardation effect, with the addition of the new and potent barrier of dormancy. Mortality was also higher at the lower temperature and, for the first time temperature has appeared as an influence capable of causing small worker-size. Do its fluctuations under natural conditions act in such a way ? The sudden appearance of the sun can cause rises of 10° C. or more in an hour under slates (Table IV) and, in woodland glades, its advent at the beginning of transit might have a similar effect. And yet if this happens to exposed nests as a result of alterations of cloud and sunlight, why are their workers not small ? *A priori*,

there seems little to support temperature fluctuation as an explanation of dwarfness.

The matter was put to the test by culturing samples in artificial nests in the field sites of interest. Each culture provided ample food and moisture, facilities for vertical migration and protection from small mammals, and they were placed either in fully insolation-exposed areas of soil or in glades in the pine plantation already mentioned. Twenty small hibernated larvae and as many workers were included in each. Cultures were set on three successive occasions at monthly intervals beginning mid-May. The material for each of the three blocks so formed was obtained from a single colony (of *Myrmica rubra*), three colonies being used in all. At each site and on each occasion cultures were duplicated; thus each block contained four cultures, two in woodland (duplicates) and two in the open (duplicates).

The expected brood retardation was evident; thus in the first group (set mid-May), by the time both exposed nests contained only pupae the shaded ones still had only larvae; but these had grown, and many were about to prepupate, although they never achieved the pupal stage (recalling the fate of prepupae under these conditions discussed earlier) and were destroyed by the workers. The second block (set mid-June) were in a larger glade, and were more successful; this block was the only one that provided enough adults for adequate size comparisons to be made. The third block (set mid-July), in spite of being in the same glade as block 2, was unable to mature adults except in the two exposed cultures; this was due to the combination of a late start, and unusually wet weather. All shaded cultures contained a residuum of larvae returned to dormancy. Thus at sub-threshold metamorphosis temperatures, larvae either grow and enter the preliminary stages of transition, later dying, or they return to dormancy. No treatment differences in head-width emerged, and hence the earlier deductions were supported and no evidence was produced suggesting that temperature, in natural conditions, affected size.

Hence the indirect insolation effect—food-supply—was next investigated. In the first experiment, under laboratory conditions, the full diet of flesh (taken by the ants from a culture of *Drosophila melanogaster*) and sugar was offered at two levels, the one ample, and the other restricted. This was combined with an investigation of the initial size of larvae, that is, the size at hibernation—although again only the smaller larvae (expected to produce workers) were used. Two initial sizes, large (L) and small (l), were combined with two food-levels F and f, to form the four combinations LF, Lf, lF, and lf. The results can be discussed under the usual three headings, colony-size, maturation rate, and worker-size (Table VIII).

The first of these, colony-size, would certainly be reduced by food-shortage, for survival was low in these cultures, and they failed to produce any eggs. In the fully-fed colonies the eggs laid by workers were numerous and yielded males. Maturation rate was also affected, although not in the same way as by low temperatures. Food restriction, instead of retarding the brood as a whole, delayed only a portion of it, the rest passing through the various stages normally. Its action was to constrict the brood "stream" rather than to dam it; and it was clear from this that the difference between shaded and exposed field nests resulted from low temperature. Analysis of variance of head-widths showed that, both food-supply and initial size gave significant effects ($P <$

TABLE VIII.—*Myrmica rubra*: Small Hibernated Larvae of Two Sizes (L and l) Cultured at 23° C. with Ample (F) and Restricted (f) Food Supply: Head-widths and Time-of-Emergence Distributions.

Head width.	Culture.			
	LF.		Lf.	
34	.	d	1	
35	cc	2	bed	3
36	aabbbb	5	acccccdd	8
37	aaabbbbbbbbbcccc	16	bbccdd	5
38	abbbb	6	bb	2
Total		29		19
Average head-width		36.9		36.2
Percentage survival		60		40
	IF.		lf.	
29	.	d	1	
30	.	—	—	
31	.	ac	2	
32	ac	2	abddddd	7
33	aaabb	5	aaabbbdd	8
34	aaaaabbbbbbb	11	acdd	5
35	aaaaaabbbbbc	12	aaab	4
36	aaaaabbbbc	10	aa	2
37	aabbb	5	.	
Total		45		29
Average head-width		34.8		33.1
Percentage survival		90		58

Each individual is represented by a letter: "a" = emerged in week 7, "b" = emerged in week 8, and so on.

Head-width in micrometer divisions (1 div. = 0.0303 mm.).

0.1 per cent.), smaller larvae and low food supply both causing small adults. The interaction was also significant ($P = 1-5$ per cent.); that is to say, food reduction caused a greater reduction in size of larvae initially small—perhaps because of a greater dependence on external as opposed to internal (reserve) food-supply. The reduction in size was about 5 per cent. of the mean size of the fully-fed ones. One further point emerged: that in food-restricted conditions, the average size of adults was smaller the later they matured.

In a further experiment, hibernated larvae of *Myrmica rubra* were cultured with ample protein (supplied as before), but either with or without sugar (sucrose). The fully-fed larvae, as is usual, were rotund, turgid and glistening, and excreted a colourless urine; but the sugar-deprived ones were creased and dull in appearance with a milky urine due to uric acid crystals. This difference is attributed to the fact that, unless sugar is available, little water other than what it receives in protein reaches the larva, for, with plenty of sugar at hand (even if dry), much water is incorporated into the larval diet as a sugar solvent. No doubt apart from this correlated factor, the sugar supply is of direct physiological benefit (*cf.* Simmonds, 1948). In sugarless cultures the workers were less active—and this in itself may account for many of the results which follow.

Lack of sugar affected maturation rate in the same way as shortage of food did—by constricting the brood stream (Table IX). Thus by the sixth week all three replicates with full food had brought brood into the adult or pupal stages, whereas in the other stages brood existed in all stages from larva to adult. Subnormality appeared in these cultures in other ways; less eggs were laid by the workers (and these later), and general survival was lower. When adult head-widths were measured, significant differences were found

TABLE IX.—*Myrmica rubra*: *Hibernated Larvae Cultured with Ample Food or with Ample Food Minus Sugar: Brood Condition after 3 and 6 weeks.*

Stage.	With sugar replicates.			Without sugar.		
	1.	2.	3.	1.	2.	3.
(a) <i>After 3 weeks</i> :						
Eggs . . .	2	15	1	0	0	0
Old larvae . .	16	12	16	28	29	26
Prepupae . .	15	14	9	1	3	2
Pupae . . .	3	8	13	0	1	0
Total old brood	34	34	38	29	33	28
(b) <i>After 6 weeks</i> :						
Eggs . . .	226	227	214	125	97	96
New larvae . .	8	14	8	0	0	0
Old larvae . .	0	0	0	1	2	3
Prepupae . .	0	0	0	0	2	2
Pupae . . .	23	16	22	11	21	8
Adults . . .	10	21	14	0	2	1
Total old brood	33	37	36	12	27	14

Initially 40 larvae and 25 workers.
Temperature constant at 23° C.

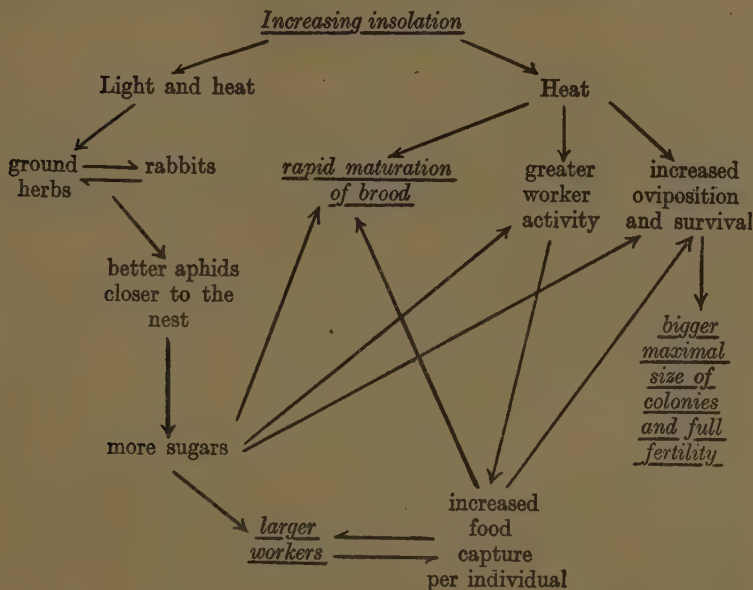
($P < 0.1$ per cent.), the sugarless cultures averaging 2–3 divisions less than the normal ones—a difference amounting to about 10 per cent. of the full size. Thus, although not essential, a sugar supply is beneficial. The wasp, *Vespula sylvestris* Scop., depends entirely on dual feeding, that is, separate sugar and protein sources, and larvae deprived of sugars soon die (Brian and Brian *in press*).

It thus appears that shortage of food in general, or merely of the carbohydrate portion, can bring about the reduction in size of worker that is required. The differences produced are moreover of the right magnitude: 5 per cent. in the first experiment (for the larvae initially smaller), and 10 per cent. in the second experiment; that is, as may be seen from fig. 1, about the difference observed between exposed and shaded colonies of 100 or more individuals.

Food-shortage may also interact with two other aspects of colony-deterioration: size and maturation rate. Although its effect on the latter is distinguishable from that of temperature, its action might be masked at low temperatures and so escape detection. Its effect on colony-size *via* survival and oviposition on the other hand cannot at present be distinguished from that of temperature (differences in the stage of death may exist), and once more,

although temperature deficiency provides an adequate explanation of small colony-size, food-supply may also be involved.

But, although it is true that food-shortage causes the formation of dwarf workers, and that temperature in natural conditions does not, it is still possible that this latter factor reduces worker activity to such an extent that food collection falls below requirements, and an *apparent* food-shortage is produced. This is most likely to affect the capture of prey, for it is known that in the wasp *Vespula sylvestris* Scop. workers lack the energy and agility needed to catch flies shortly after sunrise and before sunset. In this way, although food might be abundant in the nest vicinity, it might not be available to the ants. An environmental heat-shortage would result in starvation of brood, with the various characteristic manifestations that have been described.



This is not easy to resolve experimentally, but examination of woodland gives the impression that as regards the protein portion, food is not scarce, for Enchytriid worms, Collembola, larval Diptera, and aphids blown from trees, all of which are known to be acceptable to the species of ants concerned, are abundant. Moreover, except the Collembola, they are not particularly active animals and should be easily caught. The most likely cause of food deficiency is the absence of a plant juice supply near the nest. In the open, juices are obtained from aphids on herbs within a few feet, if not actually inside the nest,⁴ but in coniferous plantations—the form of wood most studied here—workers have to ascend the trees and visit aphids there. They are thus forced to travel

⁴ The aphids may be myrmecophilus species, principally *Tetraneura ulmifoliae* Baker and *Forda formicaria* C. Heyd, on various grasses, or adventitious species on *Succisa pratensis* Moench, *Potentilla erecta* (L.) Rausch, and *Luzula* sp.

much further and, in the lower temperatures prevailing, much slower. And so there is much evidence to the effect that the woodland ants are really short of food, but that temperature interacts by reducing activity and prolonging already long journey times.

Thus it would seem advisable to admit that the ants in woodland are probably short of food as well as being certainly short of heat. No doubt, the relative importance of these two factors will vary from year to year, and from season to season. Perhaps in the full summer months of unusually warm years the temperature régime on the wood floor may be adequate, and food alone limiting; this is especially likely if the herbs themselves are light-limited rather than temperature-limited.

The complex of interactions may be summarized by a diagram. (See p. 317.)

It is assumed that the quantity and character of the animal food supply is unchanged.

5. *Myrmica rubra*: A PHENOTYPE.

The dwarf woodland workers which have just been discussed are of the type usually allotted by taxonomists to the category *M. laevinodis* Nylander var. *ruginodo-laevinodis* Forel, but measurements have shown that spine length is reduced in the same proportion as head-width, and the woodland workers lie on the regression line relating the two for *M. rubra* L. (= *M. ruginodis* Nylander) rather than for *M. laevinodis* Nylander. In an earlier work (Brian and Brian, 1949, fig. 2, page 395) these colonies were depicted by white circles instead of black, but no biological distinction was made. The queens were typical *M. rubra macrogyna*, indistinguishable in size and other characters from those found in open habitats, and all colonies were monogynous. Thus, at any rate, some of the hitherto regarded intermediates can be classed as phenotypes of *M. rubra macrogyna*.

6. ANTS IN UNSTABLE ECOSYSTEMS.

The extensive insolation requirements of ants in the West of Scotland produce some interesting distributions, for many of the most suitable environments are transient. Two of these, the burnt-heather subseres and the felled-woodland subseres, have been studied. The biotic plagioclimax systems which these generate under the influence of mammalian grazing and browsing have also received attention but will not be referred to here.

(a) *The Burnt-heather Subseres.*

Heather (*Calluna vulgaris*) burning, if carried out in dry spring weather, may destroy all the plants. This totally barren ground is slowly recolonized by seeds of heather and herbs such as grasses, and during this phase the ants also enter. As the heather grows in height the grasses diminish, and the spreading out of the heather gradually compresses the ants which nest in the peaty surface layers of soil into the ever-diminishing bare lichen-covered areas. Nevertheless the heather growth probably improves the ant food situation, for it harbours numerous small animals in the litter at its stem bases and carries a good fauna of CERCOPIDAE. This optimum passes into a stage of shaded, cold soil as the heather extends, and all but the eurytopic *M. rubra* vanish.

This species then changes its nest site to the moss which grows in the centre of old "leggy" heather plants. The biotic plagioclimax in this subsere is chiefly sheep-walk, and is confined to the lower reaches next to agricultural land.

These stages will be illustrated by samples taken from various areas in different stages of subseral growth. All areas lay within 200 yards radius of each other. Such a method has obvious failings, but is the best that can be done at present. Permanent quadrats have been established.

The frequency of plant species is indicated by the abbreviations, and used in the same sense as Tansley (1939). Ant colonies have been roughly classified as small (less than 100 workers), medium (larger than this, but not producing sexuals), and large (that is, mature and producing sexuals).

1. Age of Subsere 2 years.

Calluna : Remains of dead burnt shrubs still littering the soil surface, with new seedlings up to 3 inches high at densities ranging from 1 to 50 per square yard. *Other plants* : Seedlings of *Festuca* sp. at densities ranging from 2 to 33 per square yard, with occasional lichens and moss, the latter especially thick on the well-compacted paths between dead old bushes. *Ants* : entirely absent in 30 samples of one yard square, taken in three sets from different areas ; this delay in colonization is a feature of the felled-woodland subsere as well.

2. Age of Subsere 4-5 years.

Calluna : shoots 9 inches long spreading out to give a height of 2-6 inches and cover 40-60 per cent. of the total area ; 5-20 per cent. of the total area covered by lichens (principally *Cladonia* sp.) or bare, and the rest a close turf of *Festuca* sp. grazed by hares and occasionally sheep. *Ants* : 30 samples taken as before (each one yard square) yielded 7 *M. rubra* colonies and 1 *M. scabrinodis* colony, well distributed. The colony of *M. scabrinodis* and 2 of the colonies of *M. rubra* were mature and had sexuals—indicating immigration of whole colonies as well as queens. Eight colonies in 270 square feet gives an area of 33.8 square feet per colony.

3. Age of Subsere 7-8 years.

Calluna : one foot high and covering 70 per cent. of the total area, with the remainder vegetated as follows : 30-80 per cent. *Festuca* sp. and the rest bare or lichen-covered ; the grasses showed signs of receding, for extensive roots and rhizomes often bore few leaves. *Ants* : a different method of sampling was used here—selected areas between the *Calluna* bushes were examined and measured. The results of 3 sets of 10 samples are summarized in Table X. In this stage the ant population is at its peak ; all species are represented, many mature colonies are present, and the average area per colony is at its lowest, being 5.2 square feet. Of the 19 colonies of *M. rubra* found, 7 were small, 8 moderate, and 4 mature, and, as one dealate female was seen running about, attempts at colonization must have been continuing. The 4 colonies of *F. fusca* included 2 small and 2 moderate—this species never attained the colony-size here that it did in the woodland stumps. Of the 5 nests of *M. scabrinodis*, 4 were mature and large and 1 moderate. Often as many as

3 colonies were found in an area, and it can readily be seen from the figures that the average number of square feet per colony *within* the open areas (about 1.6) made these appear as densely crowded "islands" in the Callunetum.

TABLE X.—*The Numbers of Ant Colonies in the Open Spaces between Heather Bushes in a 7-8-year Burn-subere.*

Species.	Set number.			Total.
	1.	2.	3.	
<i>F. fusca</i>	2	0	2	4
<i>M. scabrinodis</i>	2	0	3	5
<i>M. rubra</i> *	8	6	5	19
<i>M. sulcinodis</i>	1	0	0	1
<i>L. acervorum</i>	5	6	2	13
Total	18	12	12	42
Total area per set (square feet)	31	15	20	66

* *Var. macrogyna.*

Three sets of samples were taken.

4. Age of Subere 11-12 years.

Calluna : 15-18 inches high, spreading to cover 95 per cent. of the total area; no grasses, and the small bare or lichen-covered (*Cladonia* sp.) areas never more than 2 square feet in area, and very much shaded for the greater part of the day and the year by the neighbouring heather; in these areas *Juncus squarrosus* L. was frequent. *Ants* : the results of three sets of 10 samples are summarized in Table XI. The four common species remain, but *F. fusca* is

TABLE XI.—*The Numbers of Ant Colonies in the Open Spaces between Heather Bushes in an 11-12-year Burn-subere.*

Species.	Set of samples.			Total.
	1.	2.	3.	
<i>F. fusca</i>	1	0	0	1
<i>M. scabrinodis</i>	2	0	2	4
<i>M. rubra</i> *	4	6	2	12
<i>L. acervorum</i>	4	1	1	6
Total	11	7	5	23
Total area sampled (square feet)	13	12	10	35

* *Var. macrogyna.*

represented by a single colony, and this although situated on a slight eminence was, in respect of brood maturity, much behind normal exposed nests; unoccupied galleries were frequent and well preserved in the peat. In spite of vegetational pressure, the area per nest in the suitable positions has only fallen from 1.57 (in previous stage) to 1.52 square feet—a difference which is probably insignificant. The average total area per nest has risen to 30.4 square feet.

5. Age of Subseres 15-16 years.

Calluna: 24 inches long and bent over to cover the whole area. At the centres of these plants mosses and lichens grow with sometimes a few young heather shoots (rising from the old bases) or seedlings. This stage presumably marks the beginning of the plant climax with its internal mosaic cycles, but as the heather is normally burnt at this time, full climax is never reached. *Ants*: 100 of these mossy centres were sampled, and 15 were occupied, all by *M. rubra*. Two of these 15 were single queens, 6 were small nests, and 7 were moderate or large, so that all stages in colony growth were represented. In the lichen-covered areas previously considered this species formed 38 out of 72 nests, that is, only slightly over half; and this makes the possibility that the absence of the other 3 species is due to the chances of sampling, unlikely. There is thus good reason to suppose that *M. rubra* alone is adapted to this habitat—another example of its eurytopic character.

TABLE XII.—Summary of Heather Subseres Results.

Age of sere (years).	Area obscured by <i>Calluna</i> .	Number of species of ant.	Average area per nest (gross).	Average open area per nest (nett)
2	0	0	.	.
4-5	About 50 per cent.	2	33.8	About 17
7-8	70 „	5	5.2	1.57
11-12	95 „	4	30.4	1.52
15-16	100 „	1	.	.

Areas in square feet.

The principal features of this subserie have been summarized in Table XII. The time taken by colonies to reach maturity, even under optimal conditions, is quite unknown; a guess of between 5 and 10 years might be hazarded, for in the literature it is recorded that queens may live for longer than this. However, the ants are not entirely dependent on the satisfactory fit of their maturation cycle into the subserie cycle, for, as has been shown, they may migrate from one stage to another. Heather-moor is a mosaic of burn-subseres in different stages of regeneration.

(b) *The Felled-woodland Subserie.*

Woodland with sparse herb flora may provide, after felling, the best lowland habitat. But many factors interfere. Thus if bracken was present before felling, as is often the case in deciduous woods (except beech) with good light access to the floor, this luxuriates after cutting, and forms so dense a growth that ant life is impossible. Although the bracken itself exudes juices in early summer which are visited by ants, this plant seems singularly devoid of Hemipterous suckers to provide carbohydrate later in the year. The ground flora of *Scilla non-scripta* (L.) Hoffm. and Link and sparse *Holcus* sp. is probably equally unproductive, but no doubt the main lack is warmth, as has been shown.

Woods giving a deeper shade such as beech (*Fagus sylvatica* L.) or for other reasons maintaining a trivial ground flora, such as many conifers, provide after felling the best sites, but even these are slowly submerged by seeding birches (probably *Betula pubescens* Ehrh.), except in the places where rabbits

and roe deer (*Capreolus capreolus*) are able by browsing and grazing to maintain a plagioclimax. In such areas, which usually have the additional advantage of being well sheltered from wind by surrounding birches, the ants thrive, for these small mammals are not too heavy-footed to be destructive. Apart from the advantages of exposure which the early stage subseres provide, there are the tree stumps. These make ideal nesting sites, at first in the mosses around their bases, later under the bark that has been loosened by beetles (SCOLYTIDAE), and finally, and this much the best, in the wood itself after rot-softening has made it easily excavated. The sunny south sides of these stumps are usually occupied by large and thriving colonies.⁵

These changes have been illustrated as before by samples taken in different woodlands, felled for various periods, and lying within a radius of one quarter of a mile of each other. Permanent quadrats have been established.

1. Age of Subseres 2 years.

(a) *Stumps*: of pine, 18 inches in diameter, with the bark still adhering but undermined extensively by Scolytid beetles; fungi and general soil-fauna invading between the bark and the wood. *Surrounds*: with short moss and *Rumex acetosella* L., and further away, *Agrostis tenuis* Sibth. lightly sheep-grazed. *Ants*: of 5 stumps examined 4 had no ants, and one had a single queen, *Myrmica rubra*.

(b) *Stumps*: of beech and sycamore (*Acer pseudoplatanus* L.) in condition as above. *Surrounds*: very mixed, of *Agrostis tenuis* (f), *Holcus* sp. (f), with a variety of occasional plants including *Senecio jacobaea* L., *Pteridium aquilinum*, *Sanicula europaea* L., *Fragaria vesca* L.; grazing by rabbits only. *Ants*: on 5 stumps examined no ants were found.

These two places were so situated that colonization would necessarily be by queens and this is a slow process; where new sites are made near to well-populated ant areas, colonization includes colony immigration as well. It will be recalled that colonization of burn-subseres was comparably slow.

2. Age of Subseres 5 years.

Stumps: of pine with lichen-covered bark, still adhering; remnants of the Scolytid phase discernible, but general soil fauna largely invaded between bark and wood; mosses accumulating on axe-cut part of stump; the wood beginning to soften especially in outlying parts where roots originated. *Surrounds*: with *Rumex acetosella* (f), *Polytrichum* sp. (f), seeded birches (f) about 6 inches high, and much branched as a result of browsing, *Agrostis tenuis* (o), frond bases of the fern *Athyrium filix-femina* (L.), Roth. (o). Grazing and browsing by rabbits and roe deer. *Ants*: 10 stumps examined had from 1 to 6 nests and averaged 2.6 nests per stump (Table XIII); colonization largely by queens, but the single mature *rubra* colony almost certainly an immigrant.

3. Age of Subseres 12 years.

Stumps: principally pine, but a few oaks with the bark mostly eroded and mosses in the axe-cut; and the wood well rotted internally but often with

⁵ The density of ants off the stumps was usually so low as to be negligible in all the stages discussed here; details are given for the 12-year subseres stage in which the population was at its maximum.

TABLE XIII.—*Ant Colonies in a 5-year Felled-woodland Subere, lacking Pteridium aquilinum.*

Stump.	Species.				Total.
	<i>F. fusca.</i>	<i>M. scabrinodis.</i>	<i>M. rubra.*</i>	<i>L. acervorum.</i>	
1	—	—	—	1	1
2	1(s)	—	—	—	1
3	—	—	1(l)	—	1
4	—	—	1(m)	—	1
5	—	—	3(ssm)	1	4
6	1(m)	—	3(ssm)	—	4
7	—	—	2(mm)	1	3
8	2(ss)	2(ss)	2(ss)	—	6
9	1(s)	—	1(s)	—	2
10	1(s)	—	—	2	3
Total	6	2	13	5	26

* Var. *macrogya*.

Where more than one nest occurred in a stump, affinity was tested by mixing workers. Colony-size is indicated as follows: s = small, m = medium, and l = large. The size of colonies of *Leptothorax acervorum* could not be estimated satisfactorily.

a hard outer covering. *Surrounds*: of either *Agrostis tenuis* (d) or *Holcus* sp. (d) accompanied by birches (f) one to four feet high, *Rubus fruticosus* (f), *Calluna vulgaris* (o), *Polytrichum* sp. (o) and *Juncus conglomeratus* L. (o). Light and patchy grazing and browsing by sheep, rabbits and roe deer was causing heterogeneity, and this stage cannot be regarded as "pure" subere. *Ants*: 10 stumps examined had from 1 to 4 nests each and averaged 2.5 per stump (Table XIV). In this stage the nests were much larger, but the presence of small ones and a solitary queen indicates that colonization was still proceeding. As the stumps were the same size as before, the greater size of nests caused

TABLE XIV.—*Ant Colonies in a 12-year Felling-subere Lacking Pteridium aquilinum.*

Stump.	Species.				Total.
	<i>F. fusca.</i>	<i>M. scabrinodis.</i>	<i>M. rubra.*</i>	<i>L. acervorum.</i>	
1	1(s)	—	1(l)	1	3
2	—	1(m)	2(lm)	—	3
3	—	2(ls)	2(l1)	—	4
4	—	—	1(l)	—	1
5	—	—	2(lq)	—	2
6	1(s)	1(l)	1(l)	—	3
7	1(l)	—	—	—	1
8	1(l)	—	1(l)	—	2
9	1(l)	—	1(l)	1	3
10.	1(l)	—	1(l)	1	3
Total	6	4	12	3	25

* Var. *macrogya*.

q = Queen.

frequent proximity, and in a few, active monopolization may have taken place (e.g., numbers 4 and 7). Nevertheless, the species relative frequency does not differ significantly from that on the previous sample. This stage marks the ant climax; thereafter shrub encroachment reduces population.

In sampling the areas between stumps 30-yard square areas were examined, 3 near each of the 10 stumps. These were deliberately chosen for shortness of herb vegetation, and yet they only yielded 3 nests of *Myrmica scabrinodis* and 5 of *M. rubra*; 23 squares contained no nests, 6 contained 1 nest, and 1 contained 2 nests. Thus the average area of short herb ground per nest was 3.75 square yards. The area of a stump is about a square yard, so that the average number per stump, 2.5, represents a much higher density.

4. Age of Subseres 28–30 years.

Stumps: mainly pine and covered with a rich growth of moss (*Hypnum cupressiforme*) and lichens; moist, decaying and largely inhabited by the general soil fauna. *Surrounds*: of birch (d) in closed canopy, 15–20 feet high, with occasional oaks, ashes and sycamores up to 20 feet high; ground layer with *Agrostis tenuis* (f), *Oxalis acetosella* L. (f), *Polytrichum* sp. (f) and the ferns *Athyrium filix-femina* (o) and *Dryopteris spinulosa* (Müll.) Warr (o). *Ants*: of 10 stumps examined, 3 were without ants, but showed well-developed old galleries, 6 had only a single colony and one had 2 colonies (both *M. rubra*). *F. fusca* was absent, and there was only one *M. scabrinodis* (small), 2 *L. acervorum* and 5 *M. rubra* (3 medium, 2 small), all with small workers. It is probable that emigration from these shaded areas is impossible as the exposed plagioclimaxes are densely occupied. In only partially shaded places *F. fusca* may be found, but in very poor condition, and the situation in the birch wood must be leading by gradual elimination first of *F. fusca*, then of *M. scabrinodis* and *L. acervorum* to a sparse occupation by small colonies of *M. rubra* with small workers as in the woodland areas previously discussed, and perhaps eventually to a final elimination of all ant life.

Thus the felled-woodland subseres changes more slowly than the moorland one, and the ant population (taking the liberty of joining these samples into a sequence), reaches a climax after about 10 years. After that, it may either be smothered by birches, or be fortunate enough to persist for much longer in the plagioclimax caused by the feeding of rabbits and deer. The maximal density of colonies appears to be reached after about 5 years, and thereafter they grow in size. It might be expected that primary pleometrosis such as these species can practise would prevent over-dense "seeding"⁶ with subsequent intense inter-colonial competition. Whilst there can be no question that this unusual mechanism has an ameliorating influence, it does not seem to have acted as fully as might be thought desirable—unless two colonies per stump is more satisfactory than appears—for at 5 years, frequently 2 (but never more), small juvenile colonies of a single species existed on a single stump.

A comparison of the two subseres brings out the following points. As regards species frequency (Table XV): *M. rubra* accounts for 50 per cent. of colonies in both cases, all in the form *macrogyna*, which with its queen

⁶ The seed-dispersal analogy is of course very superficial, for it is certain that ants select their micro-habitat within the area in which they settle. To this area, however, they will certainly be influenced by wind direction and velocity.

TABLE XV.—A Comparison of Heather and Woodland Subseries in Respect of Ant Species Composition: Numbers of Colonies.

Subseries type and stage.	Species.			
	<i>F. fusca.</i>	<i>M. scabrinodis.</i>	<i>M. rubra.</i>	<i>L. acervorum.</i>
(1) Heather 2 years .	0	0	0	0
4-5 „ .	0	1	7	0
7-8 „ .	4	5	19	13
11-12 „ .	1	4	12	6
15-16 „ .	0	0	15	0
(2) Woodland 2 years .	0	0	1	0
5 „ .	6	2	13	5
12 „ .	6	4	12	3
28-30 „ .	0	1	5	2

dissemination method of reproduction makes it well adapted to seral conditions. *M. scabrinodis* likewise occupies the same status in both habitats, although at a much lower level than its congener—from 12 to 14 per cent. The situation is otherwise with the two remaining species: *F. fusca* forms 25 per cent. in woodland, and has very large colonies, but only 7 per cent. in moorland, where instead of being the second in order of abundance, it is the least common. *L. acervorum* conversely, forms 30 per cent. in moorland and only 1 per cent. in woodland.

F. fusca has, in both types of habitat, been the first species to vanish as shade encroaches, and *M. rubra*, at the other extreme, has persisted longer (and perhaps entered earlier as well) under adverse conditions, and seems to be the only species able to live in nearly-mature Callunetum. Ants clearly play no dominant part in the ecosystem here, merely assisting in a minor rôle in the circulation of essential elements. In tree stumps their excavations pave the way for destruction and erosion in various ways, principally by rabbits.

7. *Myrmica rubra*: BIMODAL WORKER HEAD-WIDTH DISTRIBUTIONS.

Fifty-one nests of *Myrmica rubra*, taken from various habitats, and from which samples of workers were taken for measurement, yielded 11 distinctly bimodal frequency distributions; of the remainder some were suggestive of bimodality, some were flat-topped, and others were simple unimodal (approximately "normal") distributions. In four of these bimodal nests separate measurements could be made of callow and older workers. When this was done, bimodality was shown to be due to different average head-widths in different age-groups. In two colonies the callows were the larger, and in two they were the smaller group:⁷ the former colonies were drawn from a felled-woodland subseries 5 years old (and therefore on the upgrade as an ant habitat), and the latter were drawn from a 14-year-old pine plantation (frequently referred to earlier in this paper), in which the trees were rapidly closing canopy. It is difficult to resist the conclusion, although the evidence is really inadequate *per se*, that the changing worker-size reflects the changing environmental fitness. It is clear from the regression of worker head-width on colony size, mentioned earlier, that growing colonies would be expected to increase worker

⁷ The actual mean differences were 0.545 mm. and 0.788 mm. (callows larger) and 1.061 mm. and 1.394 mm. (callows smaller), all highly improbable by chance.

size, but a little surprising that it should, in these cases, have happened so suddenly. In the pine plantation, even if colonies have grown to equilibrium, they may still be continually adjusting to the reduced soil insolation caused by tree growth—an adjustment ending ultimately in extinction.

These findings show the necessity for caution in interpreting polymodality of size distribution in the worker caste. In various species of ant such a configuration has been interpreted as an indication of incipient caste subdivision as for example, by Palenitschko (1927). Where age groups are few, and reared under different conditions, polymodal frequency distributions may be expected.

8. DISCUSSION.

(a) *Distribution.*

Degree of soil insolation has been shown to be a key factor controlling ant distribution in the West of Scotland; it has both a direct effect on the temperature of the nest-site, and an indirect effect on the food-supply, *via* the vegetation. Owing to the wetness of the climate and the frequency of solar screening by cloud, the four common species considered were able to extend into open, fully-exposed situations without danger of desiccation or the competition of other species, as occurs in regions of drier, warmer and longer summers (Gösswald, 1932; Talbot, 1934; Jacobson, 1939; and Westhoff and Westhoff-de-Joncheere, 1942). Whether in these cases the exposure-wards limit is determined by low moisture or by competition is unknown, but both Gösswald (1938, 1941) and Talbot (1934) have shown a correlation between distribution and resistance to desiccation, or humidity and temperature preferences. If the limit is microclimatic, then it can be paralleled in Scotland by vertical distribution, for, in the occasional periods of drought, soil under stones may become so dry that humidity in the air spaces falls below 100 per cent.; and this prevents the ants bringing their brood into temperatures desirable in moister air; in seeking warmth they are impeded by low humidity.

Ants can conveniently be pictured distributed in a sere, most simply a prisere, each species with an exposure-wards limit (or point of entry) and a climax-wards limit (or point of departure). The climax-wards limit of *Myrmica rubra* was approached with a gradual deterioration of colony and worker vitality. In our climate temperature deficiency plays an important part in bringing this about, but there is good reason to believe that food impoverishment is also involved; in fact it is doubtful if a satisfactory separation can be made. In warmer and drier regions, where air temperature is adequate in itself, the limit would be expected to be set more by food, for light-conditioned herbs would still be scarce in dense forests. But this depends on the extent to which herbs are necessary as food sources. Westhoff and Westhoff-de-Joncheere (1944) adopted the view that *M. rubra* in Holland was so dependent, for they found it in woodland as long as there were sparse herbs and mosses; but they appear to have attached no importance to the forest trees themselves in this respect. Here, workers undoubtedly ascend the trees and obtain liquids. *Formica rufa* and its allies would form an especially interesting group for investigations of this type, for they use forest tree fauna extensively, and generate heat physiologically (Raignier, 1948). Perhaps the activity of their foragers is too low, or suitable prey not available.

It is difficult to believe that ant distribution owes much to "preferences" as many authors have assumed. A group of external factors: heat and food-supply, structure and stability of the soil, weight and behaviour of grazing mammals, sites for nest construction, water-supply and competitive pressures (not predation) operating on species with different capabilities: architectural, agricultural, predatory, athletic, and aggressive, form an adequate framework on which to explain distribution. But this will receive separate and later treatment.

(b) *Insolation and the Size of Intraspecific Units.*

In section 2 a multiple regression between degree of insolation, colony-size and worker-size was considered, and the information relevant extracted. Here the relationship of the three variables can be more fully discussed. For this purpose it is more convenient and perhaps more natural, to make degree of insolation (y) into the "dependent" variable. The following standard partial regression equation is then obtained:

$$y = 0.76x + 0.16z.$$

Only the first coefficient is significant. That is to say, there appears to be no evidence of an effect of insolation on colony-size; and when it is recalled that colony-size had no effect on worker-size, only a single significant relationship is left—the influence of insolation on worker-size.

The statistical data must be considered cautiously and only in relation to other results. The absence of an effect of insolation on colony-size might be due to the interference of an additional unmeasured variable, such as competition from other colonies in the glade. This is considered unlikely as investigation failed to reveal them, but another explanation is possible.

A single relationship is unlikely to produce the two correlations, both significant (1.5 per cent. P), with a third variable (log colony size). Such systems, in which three variables all show good positive correlation, may on analysis show no partial correlation—because, if one of the three is held steady, the other two, if fully dependent cannot vary, and hence no partial correlation can occur. If inter-dependence exists but is incomplete, partial correlation may be less than simple correlation. In the case under consideration, the differences were as follows:

$$\begin{aligned} r_{xy} &= 0.852 (<1 \text{ per cent. } P), & r_{xy.z} &= 0.767 (<1 \text{ per cent. } P); \\ r_{yz} &= 0.611 (1.5 \text{ per cent. } P), & r_{yz.x} &= 0.248 (>10 \text{ per cent. } P); \\ r_{xz} &= 0.594 (1.5 \text{ per cent. } P), & r_{xz.y} &= 0.179 (>10 \text{ per cent. } P). \end{aligned}$$

The partial correlation coefficients are all smaller, the first alone remaining significant. This suggests that a large but incomplete measure of inter-dependence exists along with a close and dominating relationship, relatively independent, between insolation and worker-size; insolation affects worker-size and colony-size independently, but both interact.⁸

Apart from these considerations, all the results of the work described in this paper suggest that insolation and its derivative environmental actions (food-supply, etc.) operate in such a way as to increase colony-size. Both temperature and food-supply have been shown to affect survival and ovi-

⁸ Sewall Wright (1934) has considered similar systems in other fields of biology.

position, the optimum being 25° C. and ample food of both carbohydrate and protein types. Maximum colony-sizes may be assumed to represent a balance between these factors. Moreover, it has also been shown that colonies are smaller in woodland, and the principal difference between this environment and the outside is quantity of insolation; other factors such as higher humidity and lower wind velocity are likely to favour rather than hinder the ant populations.

There is also good reason to suppose that colony-size acts directly on worker-size. It is well known that the first workers in *Myrmica rubra* are dwarf—referred to as nanic—and in some way, during development, this condition has to change into that of large colonies with large workers. In the more open habitats it has been shown that colonization is still being attempted, and that colonies of very varying sizes, and presumably ages, exist together in a habitat. This is the case in the pine-plantation as well. In fact diversity of age structure would be the first explanation that most myrmecologists would suggest when confronted with the regression of worker-size on colony-size. The form of this regression indicates that in exposed habitats, a maximum worker-size is attained when about 500 workers are in the colony, and thereafter very little further increase takes place (fig. 1).

Exactly how worker-size is influenced by colony-size is still only partly understood. We believe that it results from a slowly shifting balance of brood interactions in the colony. Thus, a colony may be envisaged as passing through the following stages:

- (1) submaximal oviposition by the queen, workers slowly accumulating;
- (2) more workers enable more oviposition;
- (3) oviposition reaches a maximum, but survival of early brood-stages continues to improve;
- (4) both oviposition and survival being maximal, food is directed towards increasing the size of larvae and hence of workers; winged females are produced;
- (5) queen oviposition falls and she dies—colony senescence begins.

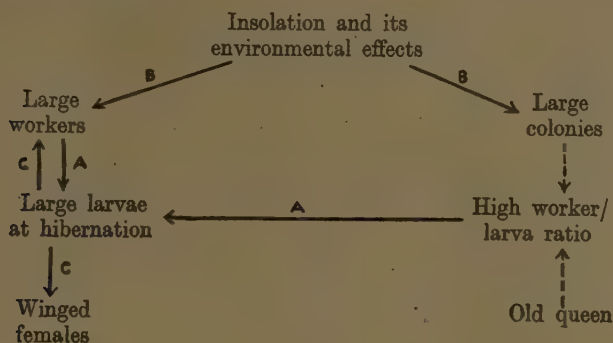
It is not intended to suggest that these events are perfectly sequential, and much overlap is to be expected.

Thus the growth of the colony brings about an increase in the worker/larva ratio, which results in an increase in worker-size. Work in progress on this aspect of ant populations has not been fully published, but enough has been, to make it worth while to construct a summarizing diagram in which full lines connect proven relations and broken lines speculative ones. It will be seen that this can be fitted on the bottom left-hand side of the earlier diagram given in section 4. The references are given in the diagram.

References are as follows: A = Brian, 1950, B = in this paper, and C = Brian (1951).

There are thus good reasons for supposing that the relationship between the three variables, insolation (*sensu lato*), colony-size and worker-size, is triangular and highly interdependent. In all habitats, variation in degree of insolation and its associated environmental effects and variation in the age of colonies will contribute towards the total variability of colony-size. This, and insolation directly, will affect worker-size; but, being interdependent, the growth of colonies and workers in a particular insolation régime will proceed simultaneously. Such a form of food-distribution is common in non-social

animals. It is interesting to note, too, that an even lower level of aggregation is simultaneously penetrated, for high food intake not only causes larger colonies and larger workers, but larger trophocytes within the workers (last observation unpublished).



9. SUMMARY.

Myrmica rubra macrogyna ranged from habitats with a fully insolation exposed, short, herb stratum into woodland with open canopy. In the latter habitat the colonies were smaller, much retarded in brood development, contained smaller workers, and were infertile, that is, produced no sexuals. In an open canopy wood, potential insolation, colony-size and worker-size were all positively correlated, and their inter-relations are discussed.

The low floor insolation caused by conifer and bracken screening reduced the temperatures prevailing to a degree deleterious to ant brood maturation; even grass, less than a foot high, has an appreciable though not as severe effect, and it was clearly demonstrated that full soil insolation was needed for ant success in the cool, wet and cloudy climate of the West of Scotland.

Three of the four signs of population deterioration (all except colony fertility) were studied experimentally. Temperature was found in laboratory experiments to account for all differences; but field experiments showed that under natural conditions worker dwarfness could not be explained in this way, and food-deficiency was thus involved. This could be real or apparent, the latter due to low temperature reducing worker activity; but after examination of the coniferous habitat, it was found that sugar sources were more distant than in the open. Hence food-shortage was probably real, though activity reduction would certainly accentuate the effects of this. Insolation thus improved conditions directly by raising temperature, and indirectly by stimulating herb growth, and so producing a proximate (and probably better) food supply.

The distribution of the four common species in man-initiated subseres has been described. Each of the two types, felled-woodland and burnt-heather, grew to an ant maximum and then declined as vegetation encroached. Ants appear as passive and transient inhabitants. The success of primary pleometrosis in preventing initial over-population is considered.

Direct evidence that in a pre-optimal subserie worker head-width was increasing, and in a growing pine plantation it was decreasing, was obtained.

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THE *CULEX PIFIENS* COMPLEX.

By P. F. MATTINGLY, LLOYD E. ROZEBOOM, K. L. KNIGHT, H. LAVEN, F. H. DRUMMOND, S. R. CHRISTOPHERS and P. G. SHUTE.

Manuscript received 22nd March, 1951.

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With 5 Text-figures.

INTRODUCTION.

By P. F. MATTINGLY.

(From the British Museum (Natural History)).

It should be made clear from the outset that my position as chairman or editor of this symposium arose from a historical accident rather than from any special knowledge of the group concerned. The symposium had its origin in an inquiry addressed to me from Kansas City as to whether a man-biting form of *Culex pipiens* which occurred there might properly be identified with our Old World "*Culex molestus*." In reply I was compelled to state that I did not know and I did not think anybody else knew either.

This is a remarkable state of affairs, because the members of the *pipiens* complex are closely associated with man and have been distinguished for a very long time. *Culex pipiens* was described by Linnaeus from Northern Europe in 1758, *Culex molestus* by Forskål from Egypt in 1785, and *Culex fatigans* by Wiedemann from the East Indies in 1828. The nomenclatorial history of the group is complicated but, fortunately, need not be discussed in detail. All that is necessary is to remark that, in general, American authors prefer to call *fatigans* "*Culex quinquefasciatus* Say." The arguments involved are not germane to the present study.

In order to help my correspondent I wrote for advice to certain persons actively engaged in studying the *pipiens* complex in various parts of the world. It is a very great pleasure to acknowledge the generosity of all those whom I approached in sending me the papers contained in this symposium, and in allowing me to use them for the discussion of the problem which took place at a meeting of the Royal Entomological Society of London on 4th October, 1950.

For a proper understanding of the problem it is necessary to know something of the distribution of the *pipiens* complex, which is a world-wide one. It will be seen from the accompanying map (fig. 1) that *pipiens* is largely a North Temperate form, though it is also said to occur widely in East and South Africa. *C. fatigans*, on the other hand, is cosmopolitan. "*molestus*" is known from Western and Central Europe, the Near East, North Africa and the Sudan. It appears to occur quite widely in the United States, and I am informed by M. Wolfs, of the Congo Medical Service, that the form of *pipiens* occurring at Costermansville agrees with it in being autogenous and in readily



FIG. 1.—Putative distribution of *Culex pipiens* and *Culex fatigans*.

biting man although it is dark in colour. It is hoped that colonies of this form may shortly be established for study purposes in this country and Egypt.

Of particular interest are those areas, shown on the map in solid black, where *pipiens* and *fatigans* occur together. They include a broad belt across the southern United States, studied by Professor Rozeboom and others, an ill-defined area in the Argentine apparently with an introduced population of *pipiens* s.l., an extensive area in Africa so far studied only at the northern end, a part of Irak and Persia, a belt running across China in an East-West direction, including the southern part of Japan and comparable with the very similar belt in the southern United States, and the area in southern Australia studied by Drummond.

The Sino-Japanese population is interesting since it includes an intermediate form known as "*Culex pipiens* var. *pallens* Coquillett." This form is mentioned several times in the following pages, and it is unfortunate that it was not possible to include a separate study of it in the symposium. The best account so far published is probably that given by Edwards in his revision of the Palaearctic mosquitoes. Further information will be found in Feng (1938).

Forms intermediate between *pipiens* and *fatigans* with respect both to colour characters and to the structure of the male terminalia have long been known to occur in California, and it is almost twenty-five years since Freeborn suggested that these might be hybrids. Nevertheless it is only recently that this suggestion has been thought to merit a fuller investigation. It is hard to resist the impression that the occurrence of hybridization in nature has been something of a skeleton in the entomological cupboard, although Edwards in *Mosquitoes of the Ethiopian Region* gave it as his opinion that the much more bizarre phenomena in *Stegomyia* spp. (Toumanoff, 1950, etc., and see Bonnet, 1950) made it seem "not unlikely . . . that hybrids between Culicine mosquitoes may occur in nature." Other authors have suggested as an alternative explanation that the Californian intermediates represent introduced "*pipiens* var. *pallens*," with which Freeborn regarded these intermediates as identical. If it is accepted that the Californian forms are hybrids then there is a *prima facie* case for the assumption that *pallens* is a hybrid also. Even on this assumption, however, it remains possible that hybridization originally occurred in one part of the range only, and was initiated in other parts of the range by the introduction of hybrid forms. The point is of some interest in considering Drummond's contribution on the subject of the southern Australian complex.

The balance of the available evidence seems to favour the view that hybridization between *pipiens* and *fatigans* does in fact occur in the Southern United States, since Sundararaman has shown that naturally occurring forms from California, Arkansas and Oklahoma are apparently indistinguishable from laboratory hybrids. Attempts to demonstrate genetical incompatibility between *pipiens* and *fatigans* have failed, and it would seem that *pipiens* from Baltimore will cross readily in either direction with *fatigans* from Texas. The hybrids have been shown to retain their intermediate character when bred in pure line, but they tend to lose it when back-crossed to either parent. They appear to be at least as vigorous as the parents. In the absence of some ethological barrier to crossing it seems that hybridization would take place

in nature. Where it did so intermediate forms might be expected to occur. The ratio of these intermediates to the typical forms would vary according to the amount of back-crossing which took place, and so would the proportion of apparently typical forms which were in fact genetically impure.

One possible barrier has been tested by Professor Rozeboom with negative results. It does not appear that either species shows any particular preference in its choice of a mate. It is possible that a difference in swarming habits might constitute an effective barrier, but this possibility could only be tested by a very thorough field study. Recent work on both Anophelini (*Anopheles labranchiae* ssp. *atroparvus*, Cambournac and Hill, 1940) and Culicini (*Aedes cantans*, Nielsen and Greve, 1950) has shown that copulation takes place very largely outside the swarm. The function of the swarm is still not understood. Nielsen and Greve suggest that it is a device for securing exogamy by mingling the males from different breeding grounds. In my opinion it may also be of importance in securing local concentrations of the species population, and thus helping to overcome the effects of the dispersive agencies by which these very small free-flying insects are affected. At all events such evidence as is available can certainly not be said to support the conclusion that swarming bears any very direct or immediate relation to individual copulation. A difference in, e.g., time of swarming would not therefore necessarily constitute a barrier to cross-breeding. It would seem desirable that if the problem is to be studied an attempt should be made to ascertain under what conditions copulation actually takes place in nature, while maintaining an open mind as to the possible relationship between this activity and swarming. For the present the production of vigorous, self-maintaining laboratory hybrids and the discovery of apparently identical forms in nature seems to afford presumptive evidence of naturally occurring hybridization, and the onus of proving the existence of ethological barriers would seem to fall on those who wish to maintain *pipiens* and *fatigans* as reproductively isolated species. The museum taxonomist has to provide a name for the specimens submitted to him, and should provide the name which the weight of the evidence appears to favour. There are no certainties in science, but for my part I am satisfied that on the evidence available *fatigans* ought to be treated as a sub-species of *pipiens*.

The nomenclature of hybrids presents some difficult problems, and there appears to be no conventional method of dealing with hybridising sub-species. In the present instance the existing vernacular name might, perhaps, be retained, at least as a temporary expedient. In the present state of our knowledge it seems that the identification of *comitatus* with *pallens* made by Dyar and Knab and by Freeborn should be accepted since no differences have been demonstrated. "*Entia non sunt multiplicanda praeter necessitatem.*" In my opinion this form should be named, both in California and in the Sino-Japanese part of its range, *Culex pipiens* var. *pallens*. The pale intermediate form described by Drummond from Melbourne should also be given this name unless and until significant differences are demonstrated. The dark Australian form does not appear, to judge from Drummond's account, to differ from the pale form except in colour. In the genus *Culex*, as in many other mosquitoes, colour characters of this kind seem frequently to vary from climatic or other extraneous causes. It seems therefore that this

may well be no more than a climatype or a form in which for some other reason the pale colour has been lost, while the pale colour of the Melbourne form would support the suggestion that it has been recently introduced. (Miss E. N. Marks, who has studied the dark form, has also suggested to me that its distribution indicates that it is an earlier introduction.) The introduction of yet another varietal name for the dark form would be most undesirable at least until it has been more fully studied.

Concerning *dipseticus*, Aitken (1942) seems to go beyond his evidence in treating this as a sub-species. The distribution of this form does not appear to have been studied in sufficient detail for it to be given a separate name, at any rate for the time being, unless, perhaps, the name *dipseticus* be used as a vernacular one. On the present evidence it seems likely that it is a hybrid of the *pallescens* type.

Among the comparative studies of the biology of *fatigans* and *pipiens* carried out in Professor Rozeboom's laboratory the serological work will be of special interest to taxonomists since it involves a comparatively new technique. (For other work of the kind on Diptera (*Drosophila*) see Cumley (1940, etc.), and for a very interesting serological study on the phylogeny of the Lagomorph mammals see Moody *et al.* (1949). West (1950) gives a general review.) It is very much to be hoped that further work of this kind will be carried out on the mosquitoes, since the precise significance of the results so far obtained cannot be assessed until a much greater body of data is available.

Of special importance for our world picture of the *pipiens* complex is the work on temperature relationships. This work has suggested to Professor Rozeboom the possible existence of a south-north cline in Nearctic *pipiens*, and it is particularly interesting to find that Laven has arrived, quite independently, at a similar conclusion regarding the Old World complex. This author's prediction of an increase in concentration of the gene for autogeny in the southern part of the range of "*molestus*" is supported by the information given to me recently by Professor Theodor of the Hebrew University of Jerusalem that all *pipiens* so far tested by him in Palestine have proved to be auto-genous. Galindo's opinion that the Californian *pipiens* population consists largely of "*molestus*" suggests a similar cline on the other side of the Atlantic.

Although the attempts to establish significant biological differences between *pipiens* and *fatigans*, described by Professor Rozeboom, have so far failed, it might be objected that a biological difference of no small magnitude is already known to occur, namely that *fatigans* readily bites man while *pipiens* does not. In this connection it is, however, important to note that until recently the idea of a specifically distinct man-biting form within *pipiens* s.l. has not been one which has commended itself to American workers and *pipiens* has very generally been treated by them as a man-biting species (i.e., as a species which *sometimes* bites man. Even *molestus* does not bite man exclusively). It should also be noted that *fatigans* does not always bite man. Non-man-biting forms are known to occur in West Africa, and have been colonized at Dakar (Mathis, 1935) and at Lagos (own unpublished observations). Galliard (1936) found that at Hanoi some *fatigans* fed indiscriminately on bird, guinea-pig or man, while others would not bite man. Some strains which would at first feed on bird or guinea-pig lost this capacity after 5 or 6 generations in laboratory colonies and would then only bite man. Wanson and Nicolay (1937) observed

the same sequence of events in Belgian Congo *fatigans* from Boma and Matadi. They further observed that *fatigans* captured in houses would not bite man in a small cage but would do so readily inside a mosquito net. From these observations it is clear that, as in other groups of mosquitoes, the phenomenon of host preference is a complex one, and that great caution needs to be exercised in treating it as a criterion of taxonomic status. It is noteworthy that many of the behaviour differences encountered in the studies here discussed are associated with differential responses to temperature, and it is possible that some confusion might be eliminated and further progress facilitated by stating the problem in these terms. Recent workers on the relation of microclimate to biting activity (Lumsden, 1947; Parker, 1948) do not seem able to agree as to the importance in this connection of host temperature. These authors, however, were concerned with *Aedes aegypti*, which appears to be a relatively indifferent species. The possibility that *pipiens* requires the stimulus of a relatively warm-blooded host (bird), while *fatigans*, in general, does not, seems worth investigating.

Of the papers relating to the *pipiens*-“*molestus*” complex of the Old World it is convenient to take first that contributed by Lt.-Cmdr. Knight, since, unlike the others, it is a summary of work already published. The results of work at present being carried out by Knight and Abdel-Malik in Egypt will be published separately and will be eagerly awaited. It is clear that the true status of “*molestus*” can only be understood by studying it in the southern part of its range. As shown by Laven, the exaggerated accounts of its differences from *pipiens* with respect to morphology and behaviour which occupy so much of the literature are attributable to the fact that “*molestus*” has mainly been studied in the northern part of its range, where ecological specialization and divergence from the *pipiens* form reach their maximum. The excellence of Knight's summary can only be fully appreciated by those whose painful task it has been to explore the labyrinthine literature on these forms.

Attempts to establish “*molestus*” as a distinct species may be said to have been prompted mainly by the fact that it exhibits certain distinctive types of behaviour. Of these the one which attracted the attention of earlier authors, such as Forskål and Ficalbi, was its readiness to bite man. As indicated above, however, this is not an absolute distinction, since *molestus* prefers to bite birds when given the opportunity. Rather it should be said that *molestus* will bite man *faut de mieux* while *pipiens*, in general, will not. From the account of the biting behaviour of *fatigans* given above it will be seen that such differences are as likely to characterize strains as species. Moreover, as shown by Professor Rozeboom, there exists in the United States an autogenous form of “*molestus*” which does not bite man. We have therefore to choose between treating “*molestus*” as a man-biting species which usually, but not always, exhibits autogeny, or placing the emphasis on autogeny, as most recent workers have done, and treating the biting habits as variable. Knight's survey shows clearly that autogeny is inherited as a mendelian recessive, and Laven has confirmed this, and shown how it accounts for the apparently sporadic occurrence of autogenous forms. As a result of some years' work on the complex as it occurs in Central Germany he has formed the opinion that the forms *pipiens* s. str. and *molestus* interbreed in nature and the gene for autogeny is freely shared between them. If this is indeed the case then a necessary criterion of

the specific status, namely, the absence of gene flow, does not, as Laven points out, exist, and the two forms must be regarded as conspecific. Since Laven's opinion is in accordance with the whole weight of experimental and observational evidence it would seem that the taxonomist ought to accept it.

With respect to the physiological significance of autogeny, it has very generally been assumed that this implies an ability to dispense with animal protein or some other nutritive substance required by anautogenous forms for egg production. As indicated by Knight, attempts to demonstrate the presence of such a factor in the larval diet have failed and there has also been some disagreement as to its existence in the adult diet. Thus Roy and Ghosh (1940) showed that *Culex fatigans* cannot produce eggs on a diet of any blood fraction or even of whole blood prevented from clotting by the addition of citrate or oxalate but with nothing subtracted. I have several times confirmed this myself with *fatigans* from Lagos, and completely failed to obtain any eggs except in one case in which a few eggs were partly matured on a diet of citrated blood. These, however, were never laid and were only discovered on autopsy. MacGregor (1930) found that sugar-containing substances when ingested by mosquitoes are passed to the oesophageal diverticula. Blood, on the other hand, is passed direct to the stomach. He suggested that for maturation of the eggs it is necessary that food should pass direct to the stomach. Roy and Ghosh (1940) confirmed MacGregor's observation as to the destination of the two kinds of food inside the mosquito, and observed that passage of blood direct to the stomach took place whether it was taken by normal biting or by imbibition from cotton-wool. Failure to mature eggs is not therefore the result of diversion of the citrated blood to the diverticula. MacGregor (1931), however, found that in *Aedes aegypti* diversion of the blood to the diverticula could be secured by adding a little glucose to it, and this resulted not only in failure to mature eggs, but also, in some cases, in the formation of a transitory fat body—a most unusual phenomenon in this species. In *aegypti* heparinized blood was passed direct to the stomach and produced maturation of the ovaries, and the same was found to be the case with *Culex pipiens*, but only when these were caught early in the year. *C. pipiens* caught in the autumn failed to produce eggs when given heparinized blood, even though they were first kept at summer temperature until the fat body had been absorbed. MacGregor inferred that a cyclical factor might be involved. Roy and Ghosh (1940) criticize his results on the ground that his "unsheathed proboscis" method of feeding leads to inconsistencies in the ultimate destination of the food inside the mosquito. They suggested that failure to produce eggs on a diet of citrated blood might be due to the fact that the actual amount of blood taken falls below the necessary minimum. Tate and Vincent, however, showed that in *pipiens* eggs could be produced, in about a quarter of the mosquitoes used, on a diet of citrated blood provided this blood was obtained from birds and not from man. The same authors obtained eggs on diets of citrated toad blood and of whole ox blood, but failed with haemolysed canary blood, citrated human blood, ox corpuscles in saline and ox serum. They failed to confirm the existence of the seasonal effect noted by MacGregor, and suggest that his negative results may have been due to the use of human blood. Reviewing this work one conclusion at any rate emerges, and this is that the physiological background to autogeny is likely to be distinctly complicated, and unless this fact is realized the egg-

maturation factor supposed to be present in the blood may prove something of an *ignis fatuus*.

With regard to other biological characters it is noteworthy that, as Knight's summary shows, stenogamy is not necessarily linked with mammal-biting, nor eurygamy with ornithophily. The association of these characters with autogeny also appears to vary, but it is not clear that adequate precautions have always been taken to ensure that so-called anautogenous forms are anything more than heterozygous populations with suppressed autogeny which would appear after breeding in the laboratory for a few generations. The so-called "*papiens* var. *berbericus*" seems to have been a case in point. Some caution should also be exercised in labelling a form as non-man-biting unless it is clear that the experiment has been performed under suitable conditions (Seaton and Lumsden, 1941; Mattingly, 1946). It is, however, quite evident that the biological characters supposed to typify *molestus* do not always appear in combination with one another, and in view of the small number of strains that have been examined it is remarkable that so many of the possible combinations have already been found. With respect to stenogamy it may be noted that some divergence in the basic ethological character exists within the form "*molestus*," since Marshall observed that in his strains the female remains resting on the substratum while the male flies round her prior to initiating the sexual act. Richards, on the other hand, discussing his Pennsylvania strain, states that the male remains at rest while the female flies round him. In its stenogamy, as in its zoophily and probably also its homodynamy, *molestus* resembles *fatigans* rather than *papiens*, for it is known that at least one strain of *fatigans* will breed readily in cages 8 in. $\times$ 6 in. $\times$ 6 in. (Roy and Majumdar, 1939).

The differences with respect to size of egg raft noticed by Jobling may perhaps be treated as a biological character, and it must be stressed that these were undoubtedly exaggerated by failure to realize the effect on the size of raft of the type of blood ingested. It would seem that Jobling's *papiens* were fed on birds and his *molestus* on man, but *fatigans* produces very much larger egg rafts on bird blood than it does on mammal blood (my own unpublished experiments), and the same has been shown to be true of "*molestus*." Roubaud and Mezger obtained more than twice as many eggs from Paris "*molestus*" fed on bird blood as from those fed on man, and in the case of "*papiens* var. *berbericus*" the ratio was more than 3 $\times$. Similarly Woke (1937) obtained a ratio of over 2 $\times$ with stream-bred man-biting "*papiens*" from Baltimore. MacGregor (1932) obtained 136-224 eggs with a mean of 150 from *molestus* fed on bird blood as compared with the 67-176 with mean of 91 quoted by Jobling.

The supposedly greater tolerance for foul water shown by "*molestus*" *vis-à-vis* *papiens* would appear to be a very dubious character, since many mosquitoes show a very great range of tolerance in such respects. In *fatigans* Senior White (1934) records a range of pH tolerance from about 1.6 (in a tank of dilute HCl in a paint works!) to 9.6. Evidence that any significant difference between "*molestus*" and *papiens* exists where both have been clearly proved to coexist and to have a free choice of breeding waters does not appear to have been produced.

Before proceeding to the morphological characters a word should be said concerning cross-breeding experiments. As Knight says, these have usually been successful in both directions, but there have been failures. Among them

the most interesting are those recorded by Marshall in strains of "*molestus*." Using four different strains from Hayling Island, Hull, Paris and Westminster respectively he was successful in making the cross in both directions only with the Hull and Paris strains. Hayling Island females produced fertile eggs only when crossed with Hayling Island males, and the other crosses were successful in one direction only. It will be seen that with respect to genetical compatibility even the form "*molestus*" is exceedingly heterogeneous. It is often said that ability to hybridize in the laboratory is no proof of conspecificity. It is equally true that isolated cases of failure to hybridize cannot of themselves constitute proof of specificity, since this is a matter of reproductive isolation as between populations, not as between individuals or groups. Thus, for example, the terminal members of a cline may be completely intersterile, while reproductive continuity is maintained through the cline as a whole by the compatibility of adjacent groups.¹

With respect to colour characters it may be said straight away that none of these is reliable. The white knee-spots favoured by some workers commonly show greater development in dark strains or individuals of the genus *Culex*, and cannot be accepted as a distinct character from that provided by the general body-colour. The pale colour commonly found in *molestus* is suggestive, particularly when taken in conjunction with the reduced response to light observed by Tate and Vincent. McEwen (1918) has described a mutation in *Drosophila* which abolishes the fly's phototropism and at the same time changes the body colour to tan. As Huxley (1942) has pointed out, such a mutation would be adaptive in dark surroundings, and it seems possible that we may be concerned with a similar mutation in *molestus*. Gilchrist and Haldane (1947) regard the mutant gene for white eye in *molestus* as probably homologous with the similar gene in *Drosophila* and their paper should be consulted for a further discussion of this point. The pale colour itself is presumably due to some irregularity in amino-acid metabolism, which may or may not be associated with autogeny. The source of the adult pigment is not known. Golberg and DeMeillon (1947) have shown that larvae of *Aedes aegypti* can be rendered almost colourless by depriving them of phenylalanine or tyrosine. The effect is transmitted to the pupa but not to the adult.

The dark spots on the sternites favoured by Sir Rickard Christophers are so variable even in this country that I do not think they would be accepted as diagnostic by anyone with experience of more than a very few strains. Moreover Roubaud and Ghelelovitch (1950) have shown that when "form *sternopunctatus*" and "form *sternopallidus*" of "*molestus*" are crossed blending occurs in the offspring, with the character "*sternopunctatus*" showing incomplete dominance.

The structure of the male palps and of the larval siphon might seem to be more promising characters, but the former has been found by Laven to be entirely worthless, and the range of variation with respect to the latter found

¹It should perhaps be stated that, since going to press, some support has been given to the suggestion that "*molestus*" may represent a complex of sibling species. On this point and on the partial or complete intersterility of geographically representative populations of *molestus* see Laven in Mattingly et al., *Trans. IXth Internat. Congr. Ent.* (In press).

by Lewis (1945) in Sudan "*molestus*" overlaps with that given by Marshall for *pipiens* s. str.

So much has already been said concerning Dr. Laven's preliminary summary that it only remains to add a few words with regard to his views on the probable distribution of autogeny among the mosquitoes. Most workers will certainly agree with him that this phenomenon must be more widespread than the few observations so far made might imply. At least two whole genera (*Megarhinus* and *Harpagomyia*) are obligatorily autogenous, and have their proboscis modified for securing nectar from flowers and from ants respectively. To the list of Culicini definitely known to be autogenous may be added *Aedes caspius* Pallas and *Uranotaenia unguiculata* Edwards, which Professor Theodor tells me he has tested with positive results in Palestine.² Reasons for supposing that, in nature, plant sugars are probably an essential part of the diet even of blood-sucking species have been given elsewhere (Mattingly, 1949, and see Wigglesworth, 1949).

The essence of Laven's argument is that in the *pipiens*-"*molestus*" complex we are faced with an assemblage of diverse genetical potentialities, the expression of which is conditioned by the selective action of the environment rather than by any limitation to cross-breeding. It appears that this conclusion is in accordance with the evidence and I am in full agreement with it. I cannot, however, accept his corollary that the idea of *molestus* as an urban biotype is wholly untenable. It seems to me that in the northern part of the range the urban environment favours the appearance of a certain combination of characters, autogeny, man-biting, stenogamy, the cryptozoic habit, which are adaptive to this environment. With these are commonly associated certain morphological characters, some of which may perhaps be genetically linked with adaptive physiological characters or themselves directly attributable to adaptive physiological processes. The result is a fairly well-defined urban biotype, which to field workers such as Mr. Shute appears highly distinctive and may well be of some medical importance. If it is of assistance to the applied entomologist to give this biotype a separate name, then it might perhaps be called "form *molestus*." It must, however, be fully realized that such a name will not imply any constancy of physiological, ethological or morphological characters outside the particular ecological niche concerned and the name should be strictly reserved for urban forms.

If, however, it is felt that the use of such names may obscure the necessity for the ecologist and the taxonomist to adopt a genetical approach to their work then I should strongly deprecate it, since this appears to me to be a *sine qua non* for the future progress of both disciplines. Darlington (1945), in discussing the necessity for a wider application of fundamental genetics, has given it as his opinion that in this country "Fundamental biology does not exist either for the botanist or the zoologist, either for medicine or agriculture. Biology teaching and research are thirty years out of date." If this is true then the study of mosquitoes has not yet progressed beyond its very early infancy. I do not think that it has.

Where this introduction may have seemed unduly discursive the intention has been to emphasise some of the possibilities implicit in the genetical

² For further additions see Mattingly et al., *Trans. IXth Internat. Congr. Ent.* (In press).

approach. Darlington's plea has been echoed with special application to the mosquitoes by Bates in *The Natural History of Mosquitoes*. The necessary cytological background has been sketched in for *pipiens* s.l. by Sutton (1942) and for *molestus* by Gilchrist and Haldane (1947). Further work on *pipiens* s.l. has been carried out by Callan and Montalenti (1947). White (1949) has related the sex-determining mechanism of Culicidae and other Nematocera to the phylogeny of the Diptera as a whole. It is evident that the absence of specialized sex chromosomes and the apparent inheritance of sex as a mendelian character under the control of a single dominant gene for male renders analogies with other groups highly dangerous. Much further work will be required before the full implications of these cytological peculiarities can be understood.

Professor Rozeboom and Dr. Laven have given their support to the views expressed by Ernst Mayr in his *Systematics and the Origin of Species* and have put forward a plea for an objective species concept in preference to one based on the subjective opinion of the taxonomist. In this I am wholly with them. As they have said, our understanding of the mechanism of evolution must depend on the study of population genetics and of the geography of small morphological variations. It cannot be too often or too strongly emphasized that the species is an actual population or group of populations existing in nature. To speak of "scientific control" when we are in complete ignorance of the minimum population size necessary for the establishment or survival of a species, of the degree of selection exercised by environmental agencies, of the distribution of infra-specific strains and of their individual and collective capacities for adaptation is surely a little premature.

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THE *CULEX PIFIENS* COMPLEX IN NORTH AMERICA.

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THERE are two widespread populations of the *Culex pipiens* complex in the United States: *C. pipiens* in the north, and a southern form which North American workers call *C. quinquefasciatus*. I am quite sympathetic with the preference of the European taxonomists for the name *fatigans*; however, for the purpose of this discussion the name *quinquefasciatus* is quite suitable, as it emphasizes the fact that I am concerned with the North American form of this mosquito. The widespread *C. fatigans* may be composed of geographical populations, and the Old World representatives are not under consideration. *C. molestus* has been reported as being also present in this country. Dyar and Knab (1909) described a race of *quinquefasciatus* from western Mexico (Baja California, Acapulco, Salina Cruz), which they named *dipseticus*; they also described *C. comitatus* from the coast region of southern California and the lower Sacramento Valley. Later these authors (1917) considered *C. comitatus* to be *C. pipiens*, independently introduced into California by commerce. Freeborn (1926) stated that *C. comitatus* was identical with *C. pipiens pallens* of Japan. Both *comitatus* and *dipseticus*, according to the literature, are intermediate in morphology between *C. pipiens* and *C. quinquefasciatus*; Freeborn suggests that "in southern California we have a blending of the species, with resultant synthetic forms that would invalidate the separation of the species." There are, therefore, four possible *C. pipiens*-complex populations in North America; typical *pipiens* in the north, *quinquefasciatus* in the south, *molestus* with an undetermined distribution and *dipseticus* (? = *comitatus*) from southern California and western Mexico. Although confusing to the taxonomist, these populations present an opportunity for most interesting studies in speciation. They may be members of a single species which is in the process of dividing into several subspecific populations. If this is true, one would expect the populations to be differentiated from one another by some minor morphological or biological characters, but that where their ranges overlap, cross-breeding would occur readily with a resultant blending of the subspecific discontinuities in the hybrids. Or, the existing populations may be so-called sibling or cryptic species. In this case they may be almost or entirely identical morphologically but separated by an impassable genetic barrier. In areas where the ranges overlap, the two species would not hybridize and would retain their distinctive features, however small. This genetic barrier might be demonstrable in the laboratory through cross-breeding experiments, which might be completely unsuccessful or produce weakened hybrid progeny; however, it must be recognized that it is possible to obtain fertile and healthy hybrids from two distinct species, such as *Aedes aegypti* and *A. albopictus*. The crux of the matter is whether, in their natural habitat, two populations will remain distinct from one

another, either because of a genetical barrier or because of behavioristic patterns which prevent cross-breeding.

In this laboratory we have been endeavoring to find whether there are adequate barriers between *C. pipiens* and *C. quinquefasciatus* in the United States to permit their recognition as separate species. So far we have tested only a few of the possible differentiating features or mechanisms, but of these none has revealed a discontinuity of sufficient magnitude to separate the populations as true species. Colonies have been established in the laboratory from the following localities: *C. pipiens* from Michigan, *C. pipiens* from Baltimore; *C. quinquefasciatus* from Galveston, Texas, and "*C. quinquefasciatus*" from the Army Medical School, Washington, D.C. The latter was thought to be true *quinquefasciatus*, having originated from stock obtained either at Gulfport, Mississippi, or Wilson Dam, Alabama. However, an examination of the male terminalia showed that the colony could be assigned with certainty neither to *quinquefasciatus* nor to *pipiens*; it appeared to be intermediate between the two, and it may have been established from intermediate stock collected at either of the above localities, or contamination could have occurred in the laboratory. With these four colonies we have sought for differentiating features through cross-breeding, temperature responses, immunity reactions, susceptibility to parasitic infections and comparative morphology.

Cross-breeding.

The four laboratory colonies were readily shown to be completely infertile. Farid (1949) carried out the cross-breeding of the intermediate Alabama "*quinquefasciatus*" and Michigan *pipiens* to the third generation; and of *quinquefasciatus* from Texas with *pipiens* from Baltimore and Michigan, and also the intermediate "*quinquefasciatus*" and Baltimore *pipiens*, through two generations. Crossing was accomplished with either sex with equal facility, and Farid states that "it was only rarely that an infertile egg raft was observed." Another of my students, Mr. Leo Kartman, has maintained hybrid progeny of *pipiens* from Baltimore and *quinquefasciatus* from Texas for eleven generations at the time of writing; Kartman's impression is that this hybrid colony is even more vigorous than the parent strains. Not only do the males of *pipiens* or *quinquefasciatus* readily fertilize the females, respectively, of *quinquefasciatus* or *pipiens*, but preliminary observations indicate that the males are unable to distinguish between the two kinds of females. For example, 25 female *quinquefasciatus* and 25 female *pipiens* were placed in the same cage, 1 cubic foot in size, with 10 male *quinquefasciatus* and left for 24 hours. The females were then dissected and examined for sperm. Of 24 *pipiens* examined, 13 were with and 11 were without sperm, and of 24 *quinquefasciatus*, 13 were with and 11 were without sperm. In another cage, 25 each of *pipiens* and *quinquefasciatus* females were exposed for 24 hours to 10 male *pipiens*: of 24 *pipiens* females dissected, 15 were with and 9 were without sperm, and of 21 *quinquefasciatus*, 9 were with and 12 were without sperm. In contrast to this, when *Aedes albopictus* and *A. aegypti*, which are closely related but distinct species, were subjected to the same experimental conditions, almost all of the females were fertilized by their own males, but not a single cross-fertilization was obtained. There is, perhaps, a mechanical bar to successful pairing, for males may be observed to attempt copulation with females of the opposite

species. It should be noted that both Toumanoff (1937, 1938) and Downs and Baker (1949) obtained cross-fertilization with these species, but presumably in these experiments no choice of females was possible. Mr. Kartman also has been able to obtain fertilization of *aegypti* females by *albopictus* males, but only after prolonged contact and without a choice of females. The mechanical bar, therefore, is not absolute, and when a choice is possible the males may be able to select females of their own species.

Temperature Responses.

The response of the four laboratory populations to lethal and sublethal temperatures was investigated by Farid (1949). *Aedes aegypti* and *Anopheles quadrimaculatus* are distinctly different in their ability to withstand five minutes exposure to high temperatures; in the former, the 50 per cent. lethal temperatures of larvae and pupae fell between 45.1 and 46.7° C., and for the latter between 42.5 and 43.8° C. But between the *Culex* populations there was no real difference. The 50 per cent. lethal temperatures after 5 minutes' exposure ranged from 42.1 to 43.0° C. for the eggs, from 41.3 to 42.3° C. for all stages of larvae, and 42.0 to 42.1° C. for the pupae. Eggs, larvae and pupae of Michigan *pipiens* and the Alabama "*quinquefasciatus*" were equally susceptible to exposure at 2.0 to 2.5° C.; at 13.5 to 14° C. the rates of development and survival of the aquatic stages were the same, and there was no essential difference between these rates at temperatures ranging from 31.5 to 33° C. One possible difference in temperature responses is indicated in Farid's experiments; at a constant temperature of 31.5 to 33° C. and a relative humidity of 93 per cent. the *quinquefasciatus* from Texas was readily able to produce fertile eggs, while only a few were obtained from Michigan *pipiens* and Alabama "*quinquefasciatus*." The former apparently is able to mate at a higher temperature than are the latter two populations. Farid suggested that this might be a mechanism for keeping *C. pipiens* out of warm regions, whereas it appeared that *C. quinquefasciatus* is prevented from colonizing the northern regions by an inability to hibernate. However, this hypothesis must be tested with further experimentation.

Immunity Reactions.

Another student in this laboratory, Commander W. K. Lawlor, U.S.N., has attempted to demonstrate a difference between northern *C. pipiens* and southern *C. quinquefasciatus* through serological means. For comparison, *Anopheles quadrimaculatus* and *Aedes aegypti* were also included in these experiments. Rabbits were immunized through a series of antigen inoculations prepared from saline extracts of macerated tissues of eggs, pupae, and adults of the four kinds of mosquitoes mentioned above. Subsequently precipitin tests were run with the antigens and the antisera. Preliminary observations showed that strong reactions could be obtained between homologous antigens and antisera. Considerable cross-reactions occurred in heterologous systems, with both adult or pupal antigens and antisera. Extensive cross-reactions also occurred between the pupal antigen of one species and anti-adult sera of the others, or between the adult antigens and the pupal antisera. To eliminate the common antigens absorption tests were performed. Antiserum for one

species was treated with heterologous antigens until precipitate was no longer produced. The precipitate was removed by centrifugation and the absorbed serum was then tested against homologous antigens. The results were summarized in Table I.

TABLE I.—Homologous Antigen Dilution Titres after Absorption of Antiserum with Heterologous Antigens.

Antiserum.	Antigens.							
	quinque.		pipiens.		aegypti.		quad.	
	Adult.	Pupal.	Adult.	Pupal.	Adult.	Pupal.	Adult.	Pupal.
quinque. anti-adult	.	0	0	0	16	.	8	32
„ anti-pupal	.	.	.	0	.	128	.	128
pipiens anti-adult	2	2	.	0	64	16	32	128
„ anti-pupal	.	8	.	.	.	1024	.	1024
aegypti anti-adult	0	8	16	4	.	0	32	8
„ anti-pupal	.	64	.	64	.	.	.	64
quad. anti-adult	128	128	64	128	32	32	.	0
„ anti-pupal	.	1024	.	512	.	128	.	.

TABLE II.—*Culex pipiens*, *C. quinquefasciatus*, and their Reciprocal Hybrids as Hosts of *Dirofilaria immitis*. The Proportion of Female Mosquitoes Exhibiting various Degrees of Filarial Development during a Twenty-day Period.

Species.	Number ♀♀ dissected.	Percentage of females.			
		Negative.	With unchanged mf. in malpighian tubules.	With developing larvae ³ .	With infective larvae in labium
<i>C. pipiens</i>	201	58.2	2.9	20.2	13.4
<i>C. quinque.</i>	210	52.3	2.3	34.2	17.1
Hybrid A ¹ (F ₂)	244	54.4	1.6	35.9	16.3
Hybrid B ² (F ₂)	210	55.2	1.4	28.1	12.3

¹ *C. quinquefasciatus* ♀♀ × *C. pipiens* ♂♂.

² *C. quinquefasciatus* ♂♂ × *C. pipiens* ♀♀.

³ Includes all larvae except those in labium.
mf. = microfilariae.

The facts brought out by this table are: (1) After treatment of *C. quinquefasciatus* antiserum with *A. aegypti* or *A. quadrimaculatus* antigens, sufficient antibodies specific for *C. quinquefasciatus* remained to produce antigen dilution titres ranging from 8 to 128 in the homologous test. On the other hand, *C. pipiens* antigens removed all the *C. quinquefasciatus* antibodies, so that no reaction occurred when this antiserum was tested with *C. quinquefasciatus* antigens. (2) Following treatment of *C. pipiens* antiserum with *A. aegypti* or *A. quadrimaculatus* antigens, antigen dilution titres in the *C. pipiens* antigen-antiserum tests ranged from 16 to 1024. *C. quinquefasciatus* antigens failed to remove all of the *C. pipiens* antibodies; however, the antidilution titre in the anti-adult homologous test was only 2, and in the anti-pupal test it was 8. (3) The *A. aegypti* and *A. quadrimaculatus* antibodies were not removed by

absorption with heterologous antigens, with the apparent exception of the *A. aegypti* anti-adult serum and *C. quinquefasciatus* antigens. However, Lawlor (1949) points out that in this instance the process of absorption involved considerable dilution of the serum. It is unfortunate that it was not possible to compare *C. pipiens* and *C. quinquefasciatus* with another species or two of *Culex* instead of with species belonging to other genera. Nevertheless, these precipitin tests furnish additional evidence of the close relation between the North American *C. pipiens* and *C. quinquefasciatus*.

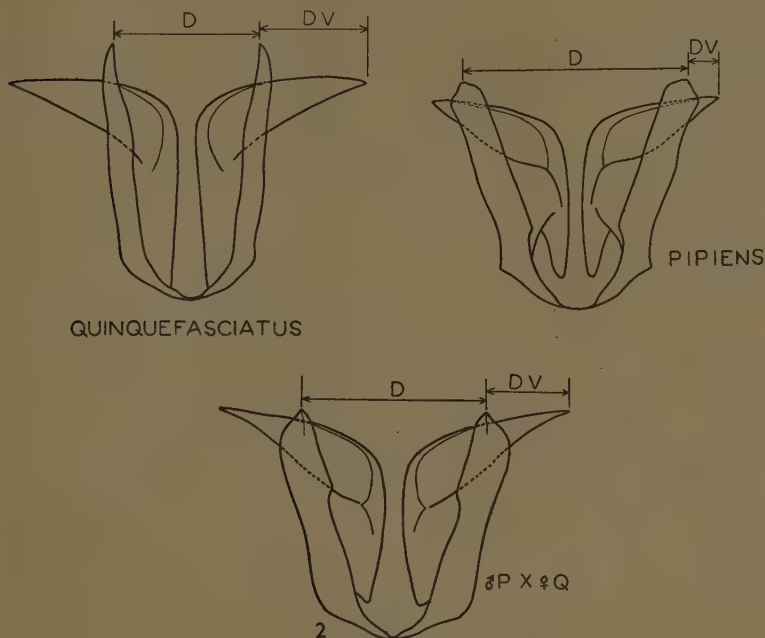


FIG. 2.—Mesosomes of *C. quinquefasciatus*, *C. pipiens* and F_1 Hybrid.

Susceptibility to Infection with Parasites.

Mr. Kartman has been investigating factors involved in the susceptibility of mosquitoes to infection with *Dirofilaria immitis*. In the course of this work he has obtained data that are pertinent to the problem under discussion. These are summarized in Table II and it will be seen that there is no difference in susceptibility to infection with the parasite between *C. pipiens*, *C. quinquefasciatus*, and hybrid progeny of these two. The tremendous variation obtained in laboratory infections of mosquitoes with various parasites warns one to be cautious in offering data such as these as evidence of similarity between two populations. Furthermore, a difference in infection rate would not necessarily mean that two groups of mosquitoes represented different species. Strains of parasites may show different infection rates in one species of mosquito. Hammon and his associates (1942-46) were unable to transmit St. Louis encephalitis

virus by *C. quinquefasciatus* from Texas, but did so with *C. quinquefasciatus* and *C. pipiens* from California. They also transmitted Japanese B encephalitis virus through *C. pipiens pipiens*, *C. pipiens molestus* and *C. quinquefasciatus*. It may be said that these virus transmission experiments and Kartman's infection experiments with *D. imitris* do not point to the separation of *C. pipiens* and *C. quinquefasciatus* as species.

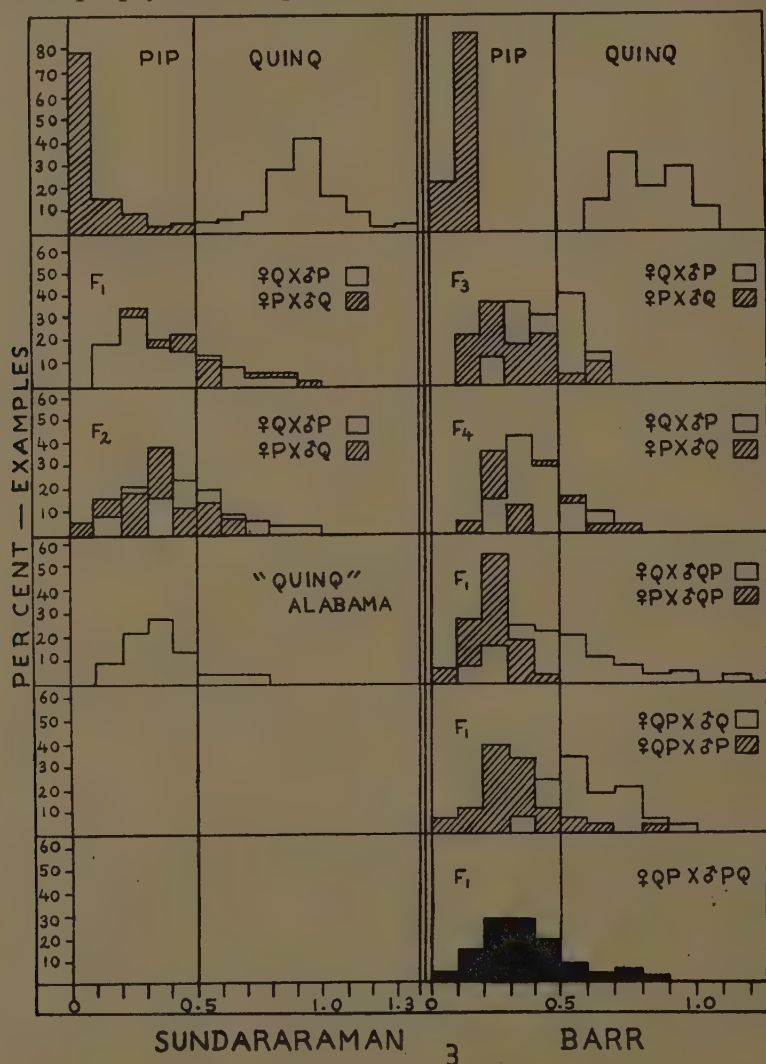


FIG. 3.—Distribution of DV/D ratios among laboratory colonies of *C. pipiens*, *C. quinquefasciatus* and hybrids.

Morphological Criteria.

Failing to demonstrate a real physiological distinction between our laboratory colonies of *C. pipiens* and *C. quinquefasciatus*, we must revert to the only means of separation available to us at present. This is a slight morphological difference in the dorsal and ventral arms of the mesosome. Sundararaman (1949) made a biometrical study of the terminalia of our laboratory colonies, and he showed that true northern *pipiens* could be separated from southern *quinquefasciatus* by the degree of outward slope of the dorsal arms of the mesosome. This, of course, is the usual key character for separating the two mosquitoes. Sundararaman expressed this character as a ratio of the distance between the tips of the dorsal and ventral arms (DV), to that between the two dorsal arms (D). Fig. 2 illustrates the mesosomes, respectively, of *C. quinquefasciatus*, *C. pipiens* and a hybrid of these two. The DV/D ratios are presented in fig. 3. Half of this figure is based upon results obtained by Sundararaman; each of his histograms is based upon 100 examples. The other half of fig. 3 presents some preliminary results obtained by another student, Mr. Ralph Barr, and are based upon 23 to 115 specimens for each histogram. Fig. 3 shows that although *C. pipiens* and *C. quinquefasciatus* are fairly distinct from one another, the hybrids are intermediate. Furthermore, this intermediacy is maintained through the fourth generation at least. There is also an indication in Barr's observations that when hybrids are backcrossed with parent strains, the character of the progeny shifts towards that of the parent.

If one holds to the concept that it is within the province of the specialist to decide whether morphological differences such as those exhibited by *C. pipiens* and *C. quinquefasciatus* determine specific rank, there is little incentive for going further with the problem. The species becomes an arbitrary unit. But if one is interested in the mechanisms by which speciation occurs, and follows a species definition such as that laid down by Mayr (1942), the significance of small morphological discontinuities in geographical populations becomes a matter of great interest.

If natural populations of the *pipiens-quinquefasciatus* complex undergo a degree of variability similar to that of our laboratory colonies, it would be impossible to draw a sharp line of distinction between them, in spite of the fact that the extreme northern and southern populations can be separated fairly accurately. Besides the intermediate Alabama "*quinquefasciatus*," Sundararaman examined a small series of wild caught males from various localities in the United States, and found intermediate forms from Osceola, Arkansas, Stillwater, Oklahoma, and San Juan Capistrano, California. The latter may be *comitatus* of Dyar and Knab. These naturally occurring intermediates are indistinguishable from our laboratory hybrids. Recent collections by the U.S. Army Fourth Service Command (see Wanamaker, Chamberlain, and Carpenter, 1944) by Quinby, Serfling, and Neel (1944), by Gurney (1943), and by Ross (1947) has revealed that there is a broad belt through the south-eastern United States where *C. pipiens* and *C. quinquefasciatus* exist side by side. If it can be shown that in these areas the two mosquitoes remain distinct, they meet the requirements for specific status. If, on the other hand, there is no barrier to hybridization with the result that there is a considerable proportion of intermediates in the natural populations, the northern and southern extremes can be nothing more than subspecies. The extent of the occurrence of natural hybrids in the

south-eastern states must still be determined, but it is quite possible, as suggested by Freeborn (1926), that in California and western Mexico the *dipseticus* and *comitatus* of Dyar and Knab are actually a hybrid population which have maintained their intermediate characteristics as our laboratory hybrid colonies have done. Galindo (1943) found that most of the wild-caught *quinquefasciatus* of California have the *dipseticus* characteristics, and he states further that "a great deal of interbreeding takes place between *molestus* and *quinquefasciatus* in California."

I have examined the slides of the male terminalia of *dipseticus* and *comitatus* in the type collection of the U.S. National Museum. The *comitatus* type closely resembles *C. pipiens*, while the mount of *dipseticus* is so poor that one could not determine the DV/D ratio.

The persistence of intermediacy in a hybrid population would probably depend upon the lack of opportunity to backcross with the parent strains. The influence of the extreme types would tend to be obscured in a predominantly hybrid population, and this may be the situation in southern California. One could also imagine that the intermediate population could be transported from its point of origin, and colonize a new area as a hybrid. This could result in the occupancy of large areas by a strictly hybrid population, and one cannot help but speculate whether this might be the origin of *C. pipiens pallens* of the Orient. In California the intermediate *comitatus* could have arisen there, resulting in a hybrid similar to that of the intermediate Oriental *pallens*, or it could have been established through introduction of *pallens* or some other hybrid. In the south-eastern United States, where both parent types exist, intermediates might tend to be obscured through introgressive hybridization.

The extent of the distribution and prevalence of *C. pipiens molestus* in North America has not been explored. Huff (1929) observed autogenous oviposition in his *C. pipiens* colonies, and later Richards (1941) recorded his observations on a colony of an autogenous, stenogamic *C. pipiens* which maintained itself in the vivarium at the University of Pennsylvania in Philadelphia. Richards also suspected the presence of this form on Long Island, New York. Galindo established a *molestus* colony from material he collected in Oakland, California; this colony interbred readily with *C. quinquefasciatus* (see Reeves and Hammon, 1946). He also believes that it is *molestus* rather than *pipiens* which is present in California. Wray (1946) established an autogenous colony from larvae collected from a water-filled hole in a tavern store-room in Illinois. The Pennsylvania strain would initiate pairing through the aggressiveness of the female; the male rested on the side of the cage, and this strain differed from European *molestus* in that it was not attracted to man as a host, whereas the Pennsylvania anautogenous form was. It is of interest to compare these habits with those of our laboratory colonies of northern *C. pipiens*. Farid (1948) noted that although pairing would occur in cages 10 by 10 by 10 inches in size, it was effected on the wing, and thus we should probably consider the strain to be eurygamous. Blood was essential for oviposition, and although we have made no direct observations on host preferences, in several years of laboratory rearing we have never observed escaped adults to feed upon us, nor to attempt to bite when the arms and hands of the experimenter were placed in the cage in the course of routine manipulations. According to Roubaud's terminology, therefore, what we would call *pipiens pipiens* appears

to be anautogenous, eurygamous, and not attracted to man. This is the form which hybridizes so readily with *quinquefasciatus*.

Richards listed several morphological differences that he observed between his autogenous *molestus* and the European *molestus*. A number of years ago I captured in my apartment in Baltimore a female *Culex* from which several generations of progeny were obtained without the feeding of blood. The adults of these mosquitoes agree well with the morphological characteristics given by Marshall (1938) for *molestus*; they are pale in colour, the banding of the tergites of the female is indistinct and not constricted, the sternites are completely white, and the first four segments of the male palpi are about equal in length to the proboscis. The biological characteristics of this autogenous strain impress one as being of a greater degree of divergence from northern *pipiens* than are those of the southern *quinquefasciatus*.

SUMMARY AND CONCLUSION.

There are four possible *C. pipiens* complex populations in North America: typical *pipiens* in the north, *quinquefasciatus* in the south, *molestus* with apparently a widespread distribution from New York and Baltimore to California, and an intermediate population in California (*comitatus*) and western Mexico (*dipseticus*).

The work in this laboratory so far has failed to reveal a distinct difference between *pipiens* and *quinquefasciatus* with respect to temperature responses, immunity reactions, or susceptibility to infection with *Dirofilaria immitis*. These two forms are completely interfertile, and 11 generations of hybrids so far obtained have been as vigorous as were the parent stocks. The males appear to be unable to distinguish between the two kinds of females.

Typical northern *pipiens* can be separated from typical southern *quinquefasciatus* by the relative positions of the arms of the mesosome. In the experimental hybrids the position of the dorsal arms is in general intermediate between that exhibited by *pipiens* and *quinquefasciatus*. Backcrossing with the parent appeared to result in a shifting of the position of the dorsal arms towards that of the parent.

Hybrids can maintain themselves as independent populations.

If it can be shown that in the areas where *pipiens* or *molestus* and *quinquefasciatus* exist side by side they remain distinct from one another, we would have to regard them as species in spite of the readiness with which they hybridize in the laboratory. If, on the other hand, they intermingle freely and produce a hybrid population, they should be considered to be subspecies. There is evidence that this is what has occurred in southern California and western Mexico; it is also possible that an already existing hybrid could be introduced into an area and establish a widespread hybrid population. The presence of intermediates in scattered localities in the south-eastern United States suggests the possibility that hybridization is occurring here also. If further work shows an extensive hybrid population in the south-eastern States we should consider our *pipiens* and *quinquefasciatus* to be subspecies.

The relationship of autogenous *molestus* in the United States to the other populations of this complex is as yet undetermined, although in California it has been shown to interbreed readily with *C. quinquefasciatus*.

It seems to me highly possible that the *pipiens-fatigans-molestus* complex

represents a cosmopolitan polytypic species. Perhaps through isolation certain populations have diverged to the point where they are marked by slight morphological or by physiological differences, but this divergence has not progressed to the point where a genetical barrier has developed. Thus, wherever conditions permit contact between recognizably distinct populations, hybridization results in the production of intermediate populations such as *pallens* of the Orient and *comitatus* or *dipseticus* in California and Mexico.

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A REVIEW OF THE *CULEX PIFIENS* COMPLEX IN THE MEDITERRANEAN SUBREGION (DIPTERA, CULICIDAE).

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INTRODUCTION.

It is now well established that two major biological forms of *pipiens* Linnaeus occur widely distributed in the Palaearctic region. These forms, variously considered species or subspecies, are treated under the names of *pipiens* L. and *molestus* Forskål by most present-day workers. In addition, other less well-known forms have been recognized, three of which have received the names of *berbericus* Roubaud, *sterno-pallidus* Roubaud and *sterno-punctatus* Roubaud.

Although much has been published on various phases of the *pipiens* complex, our knowledge of the taxonomy and biology of the included forms is still far from complete. This is due, in part to the meager morphological data available for the various forms, and in part to the absence of the necessary biological data from many portions of the geographical range. A further complicating factor is the incompleteness of our knowledge of the relationship of *pipiens* to its sister species, *fatigans* Wiedemann.

It is the purpose of this paper to review all of the diagnostic-type information available on the *pipiens* complex in the Mediterranean subregion of the Palaearctic region (as defined by Smart, 1948). For the sake of coherency it has been necessary to include information from the following European subregion countries: the British Isles, northern France, Germany, the Netherlands and Hungary.

Culex (Culex) molestus Forskål.

ADULT.—Summarized from Marshall and Staley (1937) and Jobling (1938).

Male.—First four segments of the palpi not exceeding the labium, including the labella (according to Marshall and Staley, 1935, equalling 86–100 per cent. of the length of the labium); segment III usually curved when seen from a lateral view. Scutum yellowish-brown (Ficalbi, 1893, described the scutum as being light reddish, almost rust-coloured). The dark scaling of the distal portion of the labium, the apical portion of the tergites and the dorsal surfaces of the femora and the tibiae lacking metallic blue reflections. Yellowish-white scaling at apices of femora and tibiae not visible as white dots to the naked eye. Abdominal sternites without postero-lateral patches of dark scales; median patches either absent, or else consisting of only a very few darkish scales. Ninth tergite lobes each bearing 7–15 setae (Jobling, 1938). However, in connection with these setae Marshall and Staley (1937) found averages as low as 6.8 and 7.2 for an English strain (Westminster). Their other strains (British: Hayling and Hull. France; Greece; Hungary; Malta) had averages of 9.5 to 14.7.

Female.—As in male but differing as follows: Apex of palpi sometimes having a vestige of a fourth segment (found by Jobling, 1938, in a Grecian strain and in a very few specimens of a German strain). The pale tergal bands of the female are described by Marshall and Staley (1937) as being not constricted, i.e., the basal and apical margins being straight and

parallel. However, Jobling (1938) states that the shape of the dark bands of the tergites is too variable for diagnostic use.

EGG.—Floor of micropylar apparatus with reticulations poorly defined, particularly towards the center (Roubaud, 1935). Index of greatest breadth to overall length with an average value of 0.24 (Marshall and Staley, 1935; Hayling strain). The shape of the raft and the arrangement of the included eggs are not as regular as in *pipiens* (Jobling, 1938). Often the eggs do not form rows at all. In almost every raft a number of eggs are arranged, obliquely. The shape of the raft may be rounded, square, triangular, oblong, ribbon-like or indefinite. The oblong and triangular rafts are generally laid by fed females. According to Jobling (1938), 120 rafts from unfed females contained 7–111 eggs with an average of 43, and 52 rafts from fed females contained 67–176 eggs with an average of 91. Christophers (1945) reports that the autogenous raft rarely exceeds 2 mm. in length, whereas the blood-meal raft may reach 3 mm. The total number of eggs contained in the autogenous raft and the first blood-meal raft of any single female is about equal to the total number of eggs contained in a single *pipiens* raft (Tate and Vincent, 1936).

LARVA.—Summarized from Jobling (1938). Anal papillae lengths are for larvae bred in rain-or tap-water.

First instar.—Distal portion of siphon dilated; the proximal edge of the pigmentation not sharply indicated. Siphon index 2.5–3.0, mean 2.7; length 209.1–299.3 microns, mean 265.5.

Second instar.—Siphon stout and almost straight, ventral surface straight except the most distal portion which bends inwards, dorsal surface slightly wavy. Siphon index 2.7–3.3, mean 3.0; length 426.4–508.4 microns, mean 457.2. Anal (ventral) brush with 9–19 branches, mean 13.0. Anal papillae about equal to the anal plate in length.

Third instar.—Ventral margin of siphon with a more regular curvature. Siphonal valves more or less triangular and broadly pointed from lateral view; ventral edge of valve lever with a rounded projection in middle, its dorsal edge more narrowly incurved. Siphon index 2.9–3.7, mean 3.2; length 610.5–925.0 microns, mean 746.0. Anal brush with 28–47 branches, mean 35.6. Anal papillae much shorter than anal segment.

Fourth instar.—Mentum with 18–24 teeth, mean 21 (median tooth not counted). Siphon is shorter and broader than in *pipiens*, and lacks the distinct sigmoid curve of *pipiens* because of the nearly straight dorsal surface. The valves are more or less triangular in lateral view, with a rounded apex; the valve lever narrows abruptly in two places and its narrow distal part is straight. Siphon index 3.5–4.8, means (4) of 3.9–4.4; length 1110.0–1554.0 microns, mean 1329.0. Extensive use has been made of the number of branches in the siphon hair tufts (Marshall and Staley, 1937, and Callot, 1947), but this character seems to be more indicative of local population differences than of anything else (Jobling, 1938). Anal brush with 59–90 branches, mean 70.5. Anal papillae shorter than anal segment.

VARIATIONS.—Although a number of morphological variations of the *pipiens* complex have been described, the absence of the necessary biological data in most of these cases makes it impossible at present to evaluate them. The following is the principal exception.

Lewis (1945) described the *pipiens* form occurring in the Anglo-Egyptian Sudan from Khartoum to Wadi Halfa on the Egyptian frontier as *molestus* on the basis of its man-biting habits and its breeding places (bilge-water of barges, pit latrines and in pools). No data are given concerning autogeny or steno-gamy.

Adult: General colour dark brown. First four segments of male palpi are together about equal in length to the labium, sometimes slightly shorter or longer; segment III is

somewhat curved. Number of setae on each lobe of the 9th tergite 5-16, mean 8.9. Larva : Siphon index 3.5-5.3, mean 4.3. Some larvae had a slight sigmoid curvature of the siphon. The ventral valves and the valve lever vary in shape and some specimens were of the *pipiens* type.

BIOLOGY.—*Autogeny* : Perhaps the most interesting biological diagnostic character of *molestus* is its ability to lay eggs without a previous blood meal (autogeny). The historical aspects of our knowledge of autogeny in the *pipiens* complex have been extensively reviewed by Marshall and Staley (1937) and Jobling (1938), as have the problems relating to the selection of the name *molestus* for the autogenous form of *pipiens* and the restriction of the name *pipiens* to the anautogenous form (also Natvig, 1948).

By now it seems to be well established that autogeny in *molestus* is an inherited character (Roubaud, 1930 ; Vincent, 1933 ; De Buck, 1935 ; Tate and Vincent, 1936 ; Weyer, 1935 ; and Callot, 1947), rather than solely the result of the larval diet as believed by De Boissezon (1933, 1934). In nature the percentage of *molestus* females that can lay autogenously is quite small, but the ability to do so markedly increases in succeeding autogenous-selected generations (Mathis, 1940). Hybridization experiments between *molestus* and *pipiens* have shown that autogeny always appears in at least some of the offspring, but that its appearance may be delayed until the F_2 generation (Tate and Vincent, 1936). Since it is generally conceded that hybridization between these two forms occurs in nature, the above fact would make it possible to find autogeny present in some of the offspring of anautogenous wild-caught adults (as was done by Vincent, 1933).

The exact mechanism of autogeny has not been definitely demonstrated. One widely-held opinion is that the larvae of autogenous mosquitoes store up exceptional quantities of fat body, which is carried through into the adult stage and permits the maturation and oviposition of the eggs without further nourishment (Huff, 1929 ; Roubaud, 1931, 1933, 1934 ; Roubaud and Toumanoff, 1930 ; Roubaud and Mezger, 1934a ; Hecht, 1932 ; Weyer, 1934 ; and Mathis, 1940).

Very little information is available upon the exact larval dietary requirements for autogeny, but it seems logical to believe that the larval food must be sufficiently rich in proteins and minerals to compensate for the amounts of these compounds that are normally obtained via the adult blood meal. Whatever the needed compounds are, they are apparently present in the ordinary laboratory larval diets of hay or dog-biscuit infusions, since these media prove quite satisfactory for maintaining autogenous cultures.

The maintenance of an autogenous colony by Tate and Vincent (1936) through 49 generations adequately demonstrates that the continuous use of autogenous powers does not devitalize the stock (spanogyny). Roubaud (1933) found that spanogyny did occur, but it seems likely that his cultural conditions in some way became unfavourable.

Since autogeny is not obligatory to *molestus*, it is an interesting problem as to what use *molestus* females make of a blood meal when it is taken before the initial egg laying, as they will readily do whenever it is offered. Jobling (1938) states that it not only permits the laying of a greater number of eggs but also of a greater number of viable eggs. Also, a blood meal is apparently necessary for a second (or later) egg-laying. And, of course, as with feedings

with sugar water, honey solution, sliced apple or other similar adult foods, a blood meal greatly prolongs adult life. Tate and Vincent (1936) report that autogenous females usually appear reluctant to take a blood meal before they have laid their autogenous rafts.

Copulation seems to be a prerequisite for autogenous egg-laying, as Vincent (1933) has reported that females fed on blood would lay unfertilized rafts, whereas autogenous rafts were almost invariably fertile.

Stenogamy: The ability to copulate in small spaces (stenogamy) is a second important diagnostic character for *molestus*, mating in this form having been reported in spaces as small as three cubic inches (16.39 c.c.) by Callot (1937). This is in marked contrast to *pipiens*, which requires a much larger space (eurygamy). More practical space volumes for stenogamic rearing of *molestus* range from 30 cubic inches (500 c.c.) (Marshall, 1938) to 663 cubic inches (10,867 c.c.) (MacGregor, 1932).

No definite maximum space volume has apparently been established for the diagnosis of the presence of stenogamy. However, Weyer (1935) reported that the anautogenous form would not mate in a space of 2400 cubic inches (39,336 c.c.); and Callot (1947) obtained fertilization in a eurygamous, anautogenous strain in a space of 3904 cubic inches (64,000 c.c.). Therefore, according to the results of these two investigators the minimum space requirement of *pipiens* should be somewhere between a cube of 13.5 inches and one of 15.5 inches.

Stenogamy is an inherited character. In crosses between eurygamous and stenogamous forms, stenogamy always appears in the F_1 generation (Vincent, 1933; Tate and Vincent, 1936).

In *molestus* the males copulate with resting females (Tate and Vincent, 1936); whereas in *pipiens* male swarms occur and the mating act begins in the air (Marshall, 1938).

Homodynamy: A third biological characteristic that is diagnostic for *molestus* is its ability to maintain reproductive activity throughout the year (homodynamy), as opposed to the intervention in the life cycle of a period of reproductive inactivity (heterodynamy) such as is the case with *pipiens*.

The mechanism of hibernation in mosquitoes is still inadequately known. However, according to Roubaud (1929, 1930, 1933) cyclical hibernation is obligatory in *pipiens* to allow recovery from a normally occurring specific debility. On the other hand, Bates (1949) believes it more likely that fat production (gonotrophic dissociation), and the following inactive period, is due to any combination of factors that tend to restrict the activity of the mosquito, rather than to the presence of some inner physiological rhythm. He would include here such factors as temperature and the length of the light period. As de Boissezon (1930) has pointed out, such restriction of activity probably results in a cessation of ovarian function due to the slowing down of the general metabolism, thus permitting the reserves normally used for egg maturation to be preserved and used for the survival of the hibernating female. The immediate cause of this cessation of ovarian function according to Wigglesworth (1949) is probably the failure of the corpus allatum to secrete the hormone necessary for egg production.

In view of the fact that Tate and Vincent (1936) were able to maintain a colony of *pipiens* (English strain) with the aid of artificial light and at labora-

tory temperatures through 11 generations without the occurrence of cyclical hibernation, it seems likely that the theory advanced by Bates is the more sound for this species at least.

If this theory is accepted, then it would appear that *molestus* (since it is homodynamic) should lack the ability to meet low temperatures by the production of fat body, and therefore would be less resistant to low temperatures than is *pipiens*, and that its activity should not be dependent upon the length of the daily light period. The former condition has been shown to be true in part by Jobling (1938), who found that *pipiens* is more active below 15° C. than is *molestus*. Further, it is now known that *pipiens* is probably the only subspecies in the most northern parts of Europe and that *molestus* is more common in the Mediterranean parts of the Palaearctic region (Jobling, 1938). The maintenance of *molestus* throughout the year in central Europe and in England is probably only possible because of its invasion of heated places during the winter. The second condition listed above is borne out by the fact that Jobling (1937) has shown that *molestus* can carry out complete development in total darkness.

Type of blood: A fourth biological character that has been commonly used for the separation of *molestus* from *pipiens* is host preference. Man and other mammalian animals are readily fed upon by *molestus*, whereas *pipiens* does so only rarely. This difference in feeding habits was one of the first clues to the discovery that more than one biotype of mosquito was being treated under the name *pipiens* (see Marshall and Staley, 1937, and Jobling, 1938, for the historical aspects of this problem).

In addition to mammals, *molestus* also feeds readily upon avian hosts. In connection with this it is of interest to note that bird blood results in the production of more eggs by *molestus* than does human blood (Roubaud and Mezger, 1934).

Miscellaneous: For some years *molestus* was believed to be strictly an urban species, in contrast to *pipiens*, which was regarded to be a rural species. That this distinction is no longer tenable is shown by Marshall (1938), who states, "The assumption that it is exclusively (or even chiefly) an 'urban' mosquito can no longer be supported. On the contrary, sufficient evidence has already been obtained to indicate that *C. molestus* and *C. pipiens* often co-exist in rural areas."

Another biological characteristic of *molestus* which apparently is of use in distinguishing it from *pipiens* is its ability to breed in water very rich in decaying organic material. Roubaud and Gaschen (1932) experimented with this capacity and found *molestus* more resistant than *pipiens* to solutions of human urine, ammonia, and ammonium carbonate.

DISTRIBUTION.—Using autogeny and stenogamy as the basic diagnostic characters for *molestus*, it has been definitely recorded from only the following localities in the Mediterranean subregion: France, Italy, Malta, Greece, Palestine and Egypt.

Culex (Culex) molestus var. *sterno-pallidus* Roubaud.

MORPHOLOGY.—This name was applied to the morphological variety of *molestus* in France which has the abdominal sternites without dark scaling.

Roubaud (1945) described two strains of this form, one from Aigues-Mortes and the other from the Pyrenees, which he stated differed slightly from one another biologically and morphologically.

BIOLOGY.—This variety is described as being stenogamic, homodynamic and autogenic.

Culex (Culex) molestus var. *sterno-punctatus* Roubaud.

MORPHOLOGY.—This name was applied to the morphological variety of *molestus* in France which has black spots medially on the abdominal sternites. As with *sterno-pallidus*, two strains are described. One, from Arles, showed the black spots consistently; but the other, from Paris, had these spots altogether lacking in about one-fifth of the examples. Roubaud (1945) believed this latter variation to be the result of hybridization between *sterno-pallidus* and *sterno-punctatus*.

BIOLOGY.—As with *sterno-pallidus*, this form is autogenic, stenogamic and homodynamic.

Culex (Culex) pipiens Linnaeus.

ADULT.—Summarized from Marshall and Staley (1937) and Jobling (1938).

Male.—First four segments of the palpi longer than the labium (according to Marshall and Staley, 1935, equalling 101–109 per cent. of the length of the labium in two English strains); segment III almost straight when seen from a lateral view. Scutum dark brown, in some specimens almost sepia. Distal portion of the labium, dark bands of the tergites and dorsal surface of the femora and tibiae bear very dark scales which have distinct metallic-blue reflections. White scales on apices of femora and tibiae visible as white dots to the naked eye. Sternites with median and postero-lateral patches of dark scales; the postero-lateral patches may be indistinct or absent. Ninth tergite lobes each bearing 6–11 setae, mean 8.

Female.—Apex of palpi is pointed and ends in a cup-shaped sensillum.

EGG.—Floor of micropylar apparatus with a well-defined reticulated area (Roubaud, 1935). Slenderer than the egg of *molestus*, the average value of the ratio of greatest breadth to overall length being 0.22 for an English strain (Marshall and Staley, 1935). The egg raft is symmetrical and boat-shaped, being formed of numerous eggs arranged in straight rows. One or two median rows are the longest and extend from one narrow end of the raft to the other. The majority of rafts contain from 150–300 eggs but extremes of 77 and 505 were observed (Jobling, 1938). Rafts may measure as much as 1.8×6.0 mm. in size (Christophers, 1945).

LARVA.—Summarized from Jobling (1938). Anal papillae lengths are for larvae bred in rain-or tap-water.

First instar.—The portion of the siphon beyond the constriction is funnel-shaped, and the portion before is convex ventrally and slightly concave dorsally in the middle; the proximal edge of the pigmentation is ragged and dark (more sharply indicated than in *molestus*). Siphon index 3.0–4.1, mean 3.6; length 266.5–348.5 microns, mean 310.8.

Second instar.—Siphon is slender, gradually narrowing distally and has a very slight sigmoid curvature; the ventral side is slightly concave along the basal part, whereas the dorsal side is convex on the basal half and concave distally. Siphon index 3.5–3.9, mean 3.7; length 434.8–572.5 microns, mean 473.8. Anal (ventral) brush with 8–13 branches, mean 10.2. Anal papillae are about as long as the anal segment.

Third instar.—Siphonal valves are double-pointed from lateral view. Ventral edge of valve lever is almost straight and the dorsal edge is broadly incurved. Siphon index

3.4-4.4, mean 3.9; length 703.0-925.0 microns, mean 810.3. Anal brush with 16-36 branches, mean 24.5. Anal papillae very much longer than the anal segment.

Fourth instar.—Mentum with 14-24 teeth, mean 18 (median tooth not counted). Siphon slender, gradually narrowing distally and has a slight sigmoid curvature which is much more distinct basally, where the ventral surface is concave and the dorsal one is convex. Each ventral valve is roughly rectangular with a blunt apex from lateral view. Valve lever narrows more or less uniformly towards the distal end, which is curved. Siphon index 4.5-6.4, mean 5.3; length 1184.0-1850.0 microns, mean 1573.8. Callot (1947) gave the siphon index of a French strain as 3.45-5.55 with three means of 3.8-4.15. Anal brush with 41-79 branches, mean 60. Anal papillae more than twice as long as anal segment.

VARIATIONS.—Lewis (1945) reported on 3 adults and 2 larvae from the Anglo-Egyptian Sudan (south of Khartoum) collected at 6000 to 10,000 feet elevation in the mountains. The adults were not appreciably darker than the material he felt to be *molestus*. In one male the first four segments of the palpi only just exceeded the proboscis in length. Sternites had distinct median and postero-lateral dark patches. One female had the abdominal tergite banding reduced. The number of setae on each lobe of the 9th tergite were 11-14. Siphonal indices of the two larvae were 5.8 and 6.1.

BIOLOGY.—The biological features that have thus far been found to be of diagnostic value in distinguishing between the members of the *pipiens* complex are discussed in some detail under the biological treatment for *molestus*.

Culex pipiens is anautogenous, eurygamous, heterodynamic, and ornithophilous. It is largely a rural species, and does not have the tolerance of *molestus* for larval breeding waters rich in decaying organic materials.

Although not adequately studied it is now known that more than one biotype of the anautogenous *pipiens* occurs (see the discussion of *Culex pipiens* var. *berbericus*).

DISTRIBUTION.—Anautogenous, eurygamous *pipiens* has definitely been reported in the Mediterranean subregion from France and Italy.

Culex (*Culex*) *pipiens* var. *berbericus* Roubaud.

MORPHOLOGY.—This name was applied by Roubaud (1933) to a form of the *pipiens* complex from Algeria on the basis of biological differences. No morphological data was given except that Roubaud pointed out it may correspond with the short siphon *pipiens* form recognized by Barraud (1921) in Palestine.

BIOLOGY.—This form was originally described as being anautogenous, stenogamous, homodynamous, and mammal-biting. Later, Roubaud (1939) found that it may sometimes exhibit autogeny, but attempted to explain this (1945) by saying that the involved material was probably hybrid.

Callot and Dao Van Ty (1943) found *berbericus* at Nice in southern France, differing from the Algerian material only in that it never exhibited autogeny. They also found two other strains of anautogenous, stenogamic *pipiens* in France (one at Richelieu and the other at Paris). However, these differed from *berbericus* in that they did not demonstrate any zoophilism. Roubaud (1945) suggested that the Richelieu strain must be a hybrid between *molestus* and *pipiens*, but later Callot (1947) found that its biological characters remained true through several generations. That there is a form in the United States

similar to *berbericus* is evidenced by the studies of Roth (1948) and Farid (1949), who worked with *pipiens* strains from Ohio and from Michigan and Maryland respectively and found them to be anautogenous and stenogamous (copulation occurred in spaces of 1815 and 107.5 cubic inches). In addition, pairing began in flight. No mention was made of host preferences.

A further biotype of *pipiens* was described by Roubaud (1944) from south France which combines the qualities of anautogeny, eurygamy, and anthrophilism (predilection for feeding on man).

Unnamed Morphological Varieties of the *pipiens* Complex.

(1) Theobald (1905) applied the name *quasimodestus* to a single female from Sfax, Tunis (Biro). Later Edwards (1921) described this as being a variant form of *pipiens* characterized by having the scutal scales more or less ochreous (some of the dark parts of the abdomen also tend to this colour).

(2) According to Edwards (1913) females of *pipiens* from British East Africa have extremely variable abdominal banding, being reduced in some specimens to inconspicuous pale lateral spots and with every gradation in between. Later, he (1921) stated that this variant occurred in the Mediterranean area, and Kirkpatrick (1925) specifically mentioned it as occurring in Egypt. Edwards (1921) believed it possibly to be associated with the Barraud larval variety. Still later Edwards (1926, 1941) repeated his 1913 remarks, and said that in Africa there is hardly any trace of a pale spot on the outer side of the hind tibial apex, and that the male palpi are longer than the proboscis by about one-half the length of the penultimate segment.

(3) A third variant has been described by Edwards (1921) from the Levant and Asia Minor in which the upper fork cell is shorter than usual, thus resembling *fatigans*. However, he did not find this variant in material from Mesopotamia, where both *pipiens* and *fatigans* occur.

(4) Barraud (1921) stated that *pipiens* larvae in Palestine differed from material from Western Europe and Mesopotamia (Iraq) in having a shorter siphon, a slightly smaller average number of pecten teeth, and the antennae light in colour. The abdominal bands were incomplete in some of the adults from these larvae. Edwards (1921) in speaking of this form described it as having 9-17 pecten teeth (average 12) and a siphon index of about 4.5.

Hybridization in *pipiens* Complex.

A number of investigators have performed crossing experiments between *molestus* and *pipiens* and between various strains of both forms (Vincent, 1933; Roubaud, 1933, 1945; De Buck, 1935; Tate and Vincent, 1936; Weyer, 1936; and Callot, 1947). In most cases fertile offspring have resulted from crosses of either sex, and it has been possible to show something of the genetic nature of autogeny and stenogamy, and also to hypothesize the fairly frequent occurrence of hybridization in nature. However, puzzling results have occurred in some cases, and it is clear that much more carefully-controlled experimentation is needed on this subject. Callot (1947) is practically the only investigator to have concerned himself about the results of hybridization on morphological characters, and even his work is not very conclusive, due to the fact that no very complete agreement has yet been reached on what the salient morphological characters are of *molestus* and *pipiens*.

Relationship of *pipiens* Complex to *fatigans*.

A further complicating factor in the *pipiens* complex is the close relationship of *fatigans*, which comes in contact with members of the *pipiens* complex in many portions of the world and has even been shown to produce intermediates with this complex in some of these places (Farid, 1949, and Sundararaman, 1949). Successful laboratory interbreeding between members of the *pipiens* complex and *fatigans* and the production of fertile hybrid offspring is also readily obtained (Weyer, 1936; Roubaud, 1941; Farid, 1949, Sundararaman, 1949).

In the Mediterranean sub-region the only real point of contact between the *pipiens* complex and *fatigans* known to occur at present is in lower Iraq (Mesopotamia) and in eastern Persia (Edwards, 1921); and no intermediates have yet been reported from this zone of contact (it is probable that the distribution of these two overlap in Eritrea and the Anglo-Egyptian Sudan, but these areas are on the northern edge of the Ethiopian region). However fortunate this condition is for students of the *pipiens* complex in the European and Mediterranean areas, it leaves unsettled the broader problem of terminology. Farid (1949) has suggested treating *fatigans* and *molestus* as subspecies of *pipiens* because of their proven interfertility in the laboratory, and Sundararaman (1949) has given evidence to show the presence of interbreeding in nature between *fatigans* and *pipiens*. Therefore, that the differences between these three (and the other *pipiens* biotypes that have been described) are infraspecific in character now seems to be indisputable. However, that they are all subspecies and thus fully equal in degree of evolution is impossible when the nature of the supposed differences between them are qualitatively examined.

Relationship of *Culex scotti* Theobald to the *pipiens* Complex.

This species, which is known only from the Seychelles Islands, is described by Edwards (1941) as closely resembling *pipiens* in terminalic structure. However, in ornamentation it resembles *C. musarum* Edwards or *C. ornatothoracis* Theobald. Because of the possibility that *scotti* might be a true member of the *pipiens* complex, a more detailed study of its morphology and biology certainly seems to be indicated.

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UNTERSUCHUNGEN UND DEUTUNGEN ZUM *CULEX-PIPIENS*-KOMPLEX.

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Autogenie.—Die Fähigkeit der Eientwicklung und Eiablage ohne vorherige Blutaufnahme, die sogenannte Autogenie, ist bisher nur von wenigen Stechmückenarten bekannt. Bezeichnenderweise sind es drei Arten aus drei verschiedenen Gattungen, bei denen dieses Vermögen nachgewiesen wurde, nämlich *Culex "pipiens"*, *Theobaldia subochrea* und *Aedes scutellaris*. Man könnte daraus vermuten, dass diese Fähigkeit weiter verbreitet ist, als man bis jetzt weiss, da sie über verschiedene Gattungen hinübergreift. Wahrscheinlich sind die Methoden der Zucht und Haltung der verschiedenen Arten noch zu wenig ausgearbeitet, daher unsere geringe Kenntnis über diese Frage.

Wesen der Autogenie.—Die autogenen Stechmückenarten vermögen während ihres Larvenlebens eine gewisse Menge von Reservestoffen aufzuspeichern, die nach dem Schlüpfen der weiblichen Imago in Eisubstanz umgesetzt wird. Durch schlechte Ernährung und Übervölkerung kann die Autogenie unterdrückt werden, durch reichliche Ernährung unter gewissen Voraussetzungen bei den Nachkommen eines für diese Anlage reinerbigen Tieres auf 100% oder fast 100% gesteigert werden. Dass für die Ausprägung der autogenen Eiablage die Aufnahme bestimmter Nährstoffe Vorbedingung sei, konnte nicht erwiesen werden. Vielmehr ist zu vermuten, dass diese Fähigkeit eine stammesgeschichtlich alte Anlage darstellt, die in der näheren Verwandtschaft der Culiciden noch in ursprünglicher Form vorhanden ist.

Verbreitung der autogenen Culex-Form.—Während der Nachweis der Autogenie bei *Theobaldia subochrea* und *Aedes scutellaris* nur einmal oder wenige Male im Labor gelungen ist, liegt für die autogene *Culex*-Form eine grosse Fülle von Material vor. Sie wurde gefunden in Deutschland (Neumann 1912, Hecht 1932, MacGregor 1932, Weyer 1934, eigene Untersuchungen, unveröffentlicht), Holland (de Buck 1935), Frankreich (Roubaud 1929 ff., de Boissezon 1929 ff.), England (Marshall/Staley 1935, ff.), Italien (La Face 1938), Ungarn (Vincent 1933), Griechenland (Tate/Vincent 1934), Malta (Tate/Vincent 1934), Nordafrika (Roubaud 1939, 1941), Ägypten (Kirkpatrick 1925). Danach ist die autogene *Culex*-Form von Nordafrika über Süd-, Südost- und Mittel- bis Nordwesteuropa verbreitet, anscheinend mit Schwerpunkt im Mediterrangebiet.

Die Tatsache, dass die autogenen *Culex* nach dem Absetzen ihres ersten autogenen Geleges und nach Aufnahme von Blut noch weitere Gelege machen können (bis zu 6 insgesamt, eigene Untersuchungen), und die Tatsache, dass sie, wie es den Anschein hat, besonders gern den Menschen stechen und stellenweise zu einer ausgesprochenen Plage werden, hat zu der Vermutung geführt, dass die Form noch weiter verbreitet ist, als bisher tatsächlich nachgewiesen

wurde. So liegen u.a. Angaben von *Culex*-Plagen auch aus Skandinavien (Natvig 1949) und Russland (Sawizky 1938, Kon/Dobrosmislow/Ginsburg 1942) vor, wodurch das Verbreitungsgebiet wesentlich nach Norden und Osten erweitert würde, wenn es sich tatsächlich dort um die autogene Form handelt.

Biotop.—Die Mehrzahl der Nachweise stammt aus städtischen Gebieten, wenigstens soweit es die nordwest-, west- und mitteleuropäischen Fundorte betrifft, die unter allen in der Mehrzahl sind. Das hat zu der Annahme geführt, die autogene Form sei eine Stadtmücke. Demgegenüber ist jedoch zu betonen, dass in diesen nördlichen Teilen des Verbreitungsgebietes autogene Tiere auch aus rein ländlichen Bezirken bekannt sind (England: Marshall/Staley 1935; Deutschland: eigene Untersuchungen). In städtischen Gebieten scheinen aber die Existenzbedingungen für diese Form häufiger gegeben zu sein als auf dem Lande, so dass es vorwiegend in der Stadt zur reinen Ausprägung dieser Form mit der autogenen Fähigkeit kommen dürfte. Ob sie als solche ein höheres Temperaturoptimum besitzt, das ihr in den nördlichen Teilen des Verbreitungsgebietes nur in der Stadt in gewissen unterirdischen Brutplätzen geboten wird, ist bisher noch nicht bekannt. Es besteht jedoch eine andere Deutungsmöglichkeit für diese Biotop-Gebundenheit (s.u.).

Erbgang der Autogenie.—Die Zucht der autogenen *Culex*-Form wurde erstmals von Neumann (1912) erreicht, nach der Neuentdeckung der Autogenie durch Roubaud (1929) und de Boissezon (1929) dann vielfach durchgeführt. Meist wurden autogene Stämme aus autogen abgesetzten Gelegen erzielt oder aus solchen, die von autogenen Weibchen nach Blutaufnahme gelegt waren. In einigen Fällen jedoch wurde festgestellt, dass von einer Gruppe von Weibchen, die selbst nicht autogen ablegen konnten und deshalb Blut erhielten, Tiere der F-1-Generation abstammten, die z.T. autogen waren (Vincent 1933, Weyer 1934, eigene Beobachtungen). Diese Tatsache weist auf das Vorhandensein eines erblichen Anlagenpaares Autogenie-Anautogenie hin, wobei die Anlage für Anautogenie dominant über Autogenie sein dürfte. Bei den nicht autogenen Weibchen der P-Generation, von denen autogene F-1-Weibchen abstammten, muss es sich dann um Heterozygoten gehandelt haben, die von ebenfalls heterozygoten oder auch homozygoten Männchen begattet wurden.

Der Nachweis, dass Autogenie gegenüber Anautogenie rezessiv ist, konnte in Kreuzungen zwischen autogenen und anautogenen *Culex*-Stämmen erbracht werden (Roubaud 1933, Weyer 1934, eigene Untersuchungen). Nach allen bisher vorliegenden Daten scheint dieses Anlagenpaar unifaktoriell bedingt zu sein.

Heterozygotie in Freilandpopulationen.—Die experimentelle Kreuzung zwischen autogenen und anautogenen *Culex* ist mit einer grossen Schwierigkeit verbunden. Bisher sind nur autogene Stämme bekannt geworden, die gleichzeitig auch stenogam sind. Anautogene *Culex* sind dagegen zu einem grossen Teil eurygam und nur wenige stenogame Stämme dieser Form sind bekannt (Callot/Dao Van Ty 1943, eigene Untersuchungen). Bei der experimentellen Kreuzung der beiden Formen ist also mit dieser Schwierigkeit Rechnung zu halten und deshalb sind die teilweise aufgetretenen Misserfolge bei der Kreuzung anautogener Männchen mit autogenen Weibchen wohl grösstenteils auf die Eurygamie der Männchen zurückzuführen. Die prinzipielle Möglichkeit der beiden reziproken Kreuzungen und die meist vollständige Fruchtbarkeit der F-1-Bastarde führt zu ernststen Zweifeln an der Annahme,

dass autogene und anautogene *Culex* eigene Arten seien. Durch den Nachweis von "Bastarden" in der Natur (eigene Beobachtungen) wird diese Auffassung noch stärker erschüttert. So gelang die Zucht von autogenen Tieren aus nachweislich anautogenen Elterntieren, was nur so gedeutet werden kann, dass wenigstens die Weibchen, möglicherweise aber auch die Männchen der Ausgangspopulation die Anlage zur Autogenie in heterozygotem Zustand besaßen, die bei der F-I-Generation herausspaltete. Weiterhin konnte auch durch die Kreuzung von anautogenen Weibchen aus dem Freiland (Mitteldeutschland) mit homozygot autogenen Männchen aus Laborzuchten der Nachweis erbracht werden, dass unter einer anautogenen Weibchengruppe ein Teil der Tiere die Anlage zur Autogenie in heterozygotem Zustand enthielt. Aus solchen Kreuzungen sind in der F-I-Generation entweder nur anautogene Tiere zu erhalten, dann war das Stammweibchen homozygot dominant, d.h. anautogen, oder aber ein Teil der F-I-Generation (theoretisch 50%) wird autogen, dann war das Stammweibchen heterozygot mit der rezessiven Anlage für Autogenie.

Culex molestus als Mutante von *Culex pipiens*.—Die Tatsache der Heterozygotie in natürlichen Populationen muss die Auffassung der artlichen Verschiedenheit der autogenen von der anautogenen Form, wie sie in der Benennung *Culex molestus* und *Culex pipiens* zum Ausdruck kommt, erschüttern. Das wesentlichste Kennzeichen von Arten nämlich, das Fehlen des Genflusses zwischen ihnen, ist damit nicht mehr gegeben. Die beiden Formen stehen nachweislich in Genaustausch miteinander, dessen örtliches und zeitliches Ausmass im einzelnen noch zu klären ist. Autogene und anautogene *Culex* sind danach als Mutanten der gleichen Art anzusehen.

Deutung der Verbreitung.—Diese Erkenntnisse dürften einerseits den Ausgangspunkt für eine Revision des gesamten *Culex-pipiens*-Komplexes einschliesslich *C. fatigans* abgeben, andererseits aber auch zur Deutung gewisser Verbreitungstatsachen der autogenen Form beitragen. Allem Anschein nach tritt diese im nördlichen Teile des Verbreitungsgebietes vorwiegend in solchen Biotopen auf und bleibt auch dort erhalten, wo sich aus klimatischen Gründen der ununterbrochenen Fortpflanzung kein Hindernis in den Weg stellt, d.h. dort, wo die winterliche Kälte nicht eingreift. Dort aber, wo die Winterkälte wirksam wird, führt sie zwangsläufig zur Ausmerzung der autogenen Form. Die zum Winter hin abgelegten Eier, bzw. die daraus schlüpfenden Larven müssen nämlich im Freiland zugrundegehen, deshalb die Beschränkung der autogenen Form vorwiegend auf unterirdische, nicht den jahreszeitlichen Temperaturschwankungen unterworfenen Brutplätze, deshalb auch das offenbar nur sporadische Auftreten in den Städten im nördlichen Teil des Verbreitungsgebietes. In ländlichen Gegenden dürfte es hier im Laufe des Sommers wohl zur Anreicherung der Anlagen für Autogenie in den Freilandpopulationen kommen, der Winter merzt jedoch die reinerbigen Tiere, bzw. deren Nachkommenschaft im Freiland wieder aus. Die Anlage kann hier vermutlich nur in heterozygotem Zustand in den überwinternden Weibchen weitergegeben werden.

Aus dieser Deutung ist weiterhin die Vermutung berechtigt, dass die Autogenie im Mittelmeergebiet und Nordafrika, also an der Südgrenze des Verbreitungsgebietes von *Culex pipiens* in höherem Masse in den dortigen Populationen vertreten ist, sowohl in homo- wie in heterozygotem Zustand,

weil die klimatischen Bedingungen der Existenz autogener Stämme weniger oder keinen Widerstand entgegensetzen. Eine eingehende populationsgenetische Analyse der *Culex*-Populationen entlang einer Linie von Nordafrika bzw. Ägypten über Italien-Griechenland durch Mitteleuropa bis zur Nordgrenze der *pipiens*-Verbreitung würde vermutlich zur Aufdeckung eines Gen-Gefälles für die Autogenie, eines sogen. "cline" (Huxley) führen.

Morphologische Merkmale.—Neben der Autogenie als Hauptmerkmal des sogen. "*Culex molestus*" wurden von verschiedenen Seiten auch morphologische Merkmale angegeben, die diese Form kennzeichnen sollen. Es sind dies für den autogenen *Culex* im wesentlichen die Folgenden: Hellere Gesamtfärbung, Fehlen der ventralen Fleckung auf dem Abdomen, kürzere Palpen der Männchen und relativ zur Breite kürzeres Atemrohr der Larven. Nach Roubaud (1945) und eigenen Untersuchungen sind die drei ersten Merkmale keine verlässlichen Kennzeichen. Es gibt sowohl helle, "blonde" als auch dunkle autogene *Culex*-Stämme, ausserdem kann die Ausbleichung älterer Tiere leicht irreführen. Es gibt autogene *Culex*, sowohl mit wie ohne ventrale Fleckung auf dem Abdomen und bezüglich der Palpenlänge der Männchen gibt es alle Übergänge in den einzelnen Populationen und Stämmen, so dass diese, durch Mittelwert und Streuungsmass festlegbaren Merkmale nur Populationen, nicht aber Rassen oder gar Arten kennzeichnen. Das relativ kürzere Atemrohr scheint dagegen den Larven autogener *Culex* eigen zu sein. Denkbar wäre, dass dieses Merkmal in irgendeiner Weise mit der Autogenie verbunden ist, sei es, dass das Gen für Autogenie pleiotrop ist, auf Eibildungs-Modus und Atemrohrdimensionen gleichzeitig wirkt, sei es, dass eine wirkliche, enge Koppelung zwischen benachbarten Genen vorliegt.

Die hier gegebene, von den bisherigen Aussagen abweichende Einordnung des sogen. "*Culex molestus*" als Mutante von *Culex pipiens* fusst auf allgemeinen Ergebnissen und Vorstellungen der Populationsgenetik und Evolutionsforschung. Die weitere Klärung der z.T. noch theoretischen Deutungen, die hier gegeben wurden, ist auch nur mit den Methoden der allgemeinen und insbesondere der Populationsgenetik möglich.

THE *CULEX PIPIENS* COMPLEX IN AUSTRALIA.

By F. H. DRUMMOND.

(Zoology Department, University of Melbourne.)

IN recent years a good deal of information has been published on the mosquitoes of Northern Australia, particularly on those implicated in the transmission of malaria and dengue. In the southern states, however, where, apart from a few doubtful cases of malaria, there are no known mosquito-borne diseases, the group and particularly the genus *Culex* has received very little attention.

In his account of the mosquitoes of Australasia Edwards established the wide distribution of *C. fatigans*, which he described as a "dominant domestic mosquito throughout the Australian region extending as far south as Launceston," and until recently it has been the only known representative of the *pipiens-fatigans* complex in Australia.

In 1942 a survey of the mosquito fauna of slit trenches and other breeding sites in the University grounds showed that *fatigans* was quite rare but that the genus was represented by two other forms. During the last few years *fatigans* has become plentiful and in water butts and ground water we now find three members of the complex: *fatigans*, *molestus*, and a third form which has not yet been described.

As *molestus* has not previously been recorded from Australia it is worth remarking that the identification is based on biological as well as morphological features. It is anthophilic, and laboratory experiments have shown it to be autogenous and stenogamous. The scanty records so far available indicate a distribution over the southern part of Victoria up to sixty miles north of Melbourne. It has not been recorded from the more northern states and almost certainly is not present there.

The question then arises: is *molestus* a recent introduction to this country or has it been established here over a long period and remained unnoticed because of its close similarity to *fatigans*? No systematic collections of mosquitoes from Victoria are available to check this point, and local records are unreliable because of the general assumption that *fatigans* was the only domestic species of *Culex* present here. However, the distribution of *molestus* in Australia suggests that it is a recent arrival, for it seems improbable that, if long established, it should be restricted to the colder southern part of the continent. There are no major topographical barriers to prevent its spread northwards to areas which, judged by the general distribution of *molestus* would be more favourable to it.

It is possibly significant that *molestus* was discovered here shortly after the first large scale entry of American troops into Melbourne. At this time also there was a great increase in the air traffic between the two countries.

A point of special interest is the impact of *molestus* on the native *fatigans*. As stated earlier, *fatigans* was uncommon in Melbourne in 1942-43, but the

specimens caught could be separated from *molestus* without difficulty. This was also true of *fatigans* material sent from Sydney and Brisbane. Males could be identified by the structure of the hypopygium and females by the venational character, viz., the length of cell R2 relative to its petiole (Table).

Ratio of Length of Cell R2 to Length of its Petiole in the Female Wing.

	Number.	Range.	Mean.
<i>C. fatigans</i> *	50	2.1-3.5	2.8 ± 0.3
<i>C. molestus</i>	50	4.5-6.2	5.2 ± 0.5

* Specimens from Sydney and Brisbane.

This was the situation in 1942-43. At the present time the position is complicated by the occurrence of intermediates. These have been recorded in other parts of the world, notably in California where according to Galindo "a great deal of interbreeding takes place between *molestus* and *quinquefasciatus*." This is not surprising. Interbreeding occurs readily in the laboratory, and since, in Melbourne at any rate, the immature stages of both forms occupy simultaneously the same breeding sites, the only apparent barrier to crossing would be a psychological one, i.e., a preference for intraspecific mating. The ease with which the *molestus-fatigans* cross can be obtained in the laboratory indicates that this is not a serious barrier, but it would be interesting to repeat Rozeboom's work on mating preferences, using *molestus* in place of *pipiens*.

The present evidence, then, suggests that *molestus* is a recent introduction to Victoria, that it may be expected to extend its range northwards and that it will interbreed with *fatigans*.

In addition to *fatigans* and *molestus* there is a third domestic *Culex*, at present undescribed, but clearly belonging to the *pipiens-fatigans* complex.

It has a general resemblance to *pipiens*. The dorsum is dark brown and the scales of the distal bands of the abdominal tergites and also those of the upper surfaces of the tibiae and femorae are almost black. There are prominent median and lateral patches of dark scales on the sternites. It differs from typical *pipiens* on three important points: The cell-petiole ratio in the female wing is 3.5 (2.8-4.1); the male palps exceed the length of the labium by only approximately half the length of the last segment; in the male hypopygium the second division of the mesosome is broader than in *pipiens* while the third division is less stout. In these points it approaches *fatigans*. It is, however, easily distinguished from *fatigans*, and also *molestus*, by virtue of its dark colour.

It is widely distributed in Australia, having been recorded from Victoria, New South Wales, Queensland and Western Australia. Unfortunately little is known of its biology. The immature stages are sometimes found in company with those of *molestus* and *fatigans* but are more abundant in clean water from which the others are absent. The adults are sometimes found in houses but, as far as I am aware, do not attack man. The few laboratory observations available do not lead to any definite conclusion as to their feeding habits or mating behaviour. All that can be said is that they did not breed in conditions which were more suitable for *molestus* and *fatigans*.

In several respects this mosquito is intermediate between *pipiens* and *fatigans*. The structure of the male hypopygium is of particular interest because similar, if not identical modifications of the *pipiens-molestus* condition are found in the oriental *p. pallens* and also in *molestus-fatigans* hybrids. The Australian form is distinguished from these by its dark colour. It appears to stand in the same relationship to *pipiens* as *p. pallens* does to *molestus*. If, as Rozeboom suggests, *pallens* originated as a *molestus-fatigans* hybrid, then the Australian form may have arisen as a *pipiens-fatigans* hybrid. Another possibility is that we have here an example of two primarily physiological species (*pipiens* and *molestus*) undergoing similar morphological changes to produce corresponding races.

NOTE ON MORPHOLOGICAL CHARACTERS DIFFERENTIATING
CULEX PIPPIENS L. FROM *CULEX MOLESTUS* FORSKÅL
AND THE STATUS OF THESE FORMS.

By BT.-COL. SIR S. R. CHRISTOPHERS, C.I.E., O.B.E., F.R.S., I.M.S.(retd.).

As a contribution to knowledge of *Culex pipiens*-like forms I have recently studied the differential morphological characters of an autogenous and an anautogenous strain. The materials comprised (1) a strain of which, under the name of *Culex molestus*, I gave a description of the egg-raft as contrasted with that of wild *Culex pipiens* (Christophers, 1945). I have also examined material possibly originally from the same strain kindly supplied to me from the London School of Hygiene where it is being maintained; and (2) an anautogenous series bred from a single female caught in a garden shed in Cambridge which laid a typical egg-raft as previously described by me, and the resulting adults from which were shown not to be autogenous and to be non-man-biting. Incidentally the female was caught at the same place as and under identical conditions with the wild strain previously dealt with in my paper.

In the present note I am concerned only with such morphological characters as might seem to decide the relationship of these two forms. Before giving my results, however, it seems desirable to outline very briefly what Marshall and Staley have said in this respect in their paper dated 1937. They have summarized their work on the species and have given a very clear statement of their reasons for regarding the two forms as distinct species, and for assigning to the autogenous form the designation *Culex molestus* Forskål. In any discussion regarding the relationship of these forms the points so fully established by these authors should not be overlooked.

They give a succinct account of the historical developments leading up to the present recognition of the two forms. Very briefly, in 1893 Ficalbi had given his opinion that a species of *Culex* existed in Europe which had hitherto been undetected owing to its close resemblance to *Culex pipiens* Linnaeus. He considered that there were two forms included in *Culex pipiens* as then recognized, viz., (1) a man-biting form (*haematophagus*), which, as it will appear, he wrongly took to be *Culex pipiens* L., and (2) a form which did not bite man (*phytophagus*). The description given, so far as it went, was similar to that later given by Marshall and Staley to *C. molestus* and *C. pipiens* respectively. In the main Ficalbi's differentiation of characters was into a generally paler form (*haematophagus*) and a darker form (*phytophagus*). Grassi, 1923, also noted a paler and a darker form of *C. pipiens* in Italy, the former attacking man.

Fresh interest was aroused in regard to *Culex pipiens* by Roubaud's discovery of a form obtained by him near Paris which laid eggs without a blood meal. To this character, which he regarded as a biological variation in the species, he gave the name autogeny, the form he described being *C. pipiens autogeneticus*. The same form showed another marked departure in its

behaviour in that, unlike the normal *C. pipiens*, which will not mate in a small cage, it readily did so, this property being given the name of stenogamy by Roubaud. Roubaud's work led to the finding of similar strains in different countries in Europe and a number of these were closely studied by Tate and Vincent, 1936.

The authors who appear first to have studied with any detail the morphological characters of the two forms were Marshall and Staley, who in a number of publications gave features in which these forms differed and gave to the man-attacking form the designation *Culex molestus* Forskål, and, as previously noted, summarized their findings and reasons for the identification given in their paper dated 1937. Briefly stated the points of differentiation they give are as follows :

Culex pipiens.

Adult darker. Sternites with conspicuous median and lateral patches of dark scales. See also other points given later below.

Combined length of first four segments of male palpi exceeding overall length of proboscis.

Setae on lateral lobes of ninth tergite numbering 8 or 9.

Siphon of fourth instar larva more attenuated ; siphonal index 5 or nearly so. Siphonal tufts with on average smaller total number of branches.

Egg-rafts larger, oval.

Eggs narrower.

Culex molestus.

Adult lighter. Sternites without or with only inconspicuous patches of dark scales.

Length of these segments do not exceed length of proboscis.

Setae usually 12 or more.

Siphonal index about 4. Siphonal tufts with rather larger average of total tufts.

Egg-rafts smaller, triangular.

Eggs somewhat stouter.

The following are the results of my investigation in these and other respects :

Adult ornamentation.—The strain of wild *Culex pipiens* was in general obviously darker, though bred under the same conditions as the autogenous form. This was very distinctly shown when dealing with material that had been left overnight in potash. The chitinous skeleton also seemed somewhat denser and more robust. Whilst there might have been a slight difference in tint of the thorax and more prominent knee-spots in the case of the wild *Culex*, neither character appeared to be sufficiently critical to make practical use of. The same applied to the banding of the abdominal tergites or the darker leg markings. It was otherwise, however, with the median ventral patches of dark scales on the abdomen. In fresh material these gave at once a precise and immediate differentiation. The importance of these patches in another respect will be referred to again later. Unfortunately in dried material the venter is usually shrunk and largely obscured by the turned-in edges of the tergites, so that it requires careful orientation of the specimen to display the patches even if this is possible. It can usually, however, be noted whether the venter is pale or dark.

I do not understand to what Marshall and Staley refer when they speak of lateral dark markings in this position. In both forms the pale basal bands on the tergites are continued fairly uniformly across the greater part of the

tergite visible from the dorsal aspect, but laterally they are expanded in a posterior direction down the side of the tergite to give a triangular pale area. Especially in the more posterior segments this pale area in the autogenous form is continued well down the segment, and may eliminate the dark scaling on the edge of the tergite where this is turned in ventrally. It is the median patches, however, which so strikingly differentiate the forms.

Male palpi.—The following measurements were made on a small number (20) of each species mounted in Bhatia's medium after overnight in 10 per cent. potash :

	<i>Culex pipiens</i>	<i>Culex molestus</i>
Measurements in mm.:		
Proboscis from extreme base to tip of labella.	2.54	2.40
Palps to tip of segment 3*	1.90	1.80
„ segment 4	0.70	0.56
„ segments to tip of 4*	2.60	2.36
„ segment 5	0.82	0.59
Proportions :		
Palps 1-4/proboscis	1.02	0.98
„ 1-3/segm. 4	2.71	3.21
„ 1-3/ „ 5	2.32	3.05

* Measured from level of base of proboscis.

Inspection without exception gave the appearance that segments 1-4 definitely extended further than the tip of the proboscis in *C. pipiens*, whereas in the autogenous form they appeared not to do so. Actual measurements gave the figures 1.02 as against 0.98 respectively for the mean and there was little actual individual departure. The difference is mainly due to the greater length of segment 4 in *C. pipiens*. In the units used for measurement this measured in all specimens of the autogenous 1.0 or under, whilst in *C. pipiens* in 12 out of the 20 it was 1.2, the remaining measurements being 1.25 in 4 and in 1.15 in 4. As noted in the table, the relative length of this segment to that of segments 1-3 gave a very distinctive result, viz., 2.71 as against 3.21 in the autogenous form. Segment 5 is also longer in *C. pipiens*, the proportion to 1-3 being 2.32 as against 3.05 in the autogenous form.

The female hypopygium.—The main features are very similar in the two forms. A proctiger consisting of a flap-like conical postgenital plate (eleventh sternite) and two lobed hairy cerci is at the base ringed by a narrow ribbon of chitin forming the ninth tergite and cowl, whilst lying just anterior to this is the ninth sternite with at the middle point of the latter a small setigerous lobe, the insula. A conspicuous horse-shoe-shaped structure lying internally and anterior to the insula is probably the vaginal apodeme. The most likely structures to show differences seemed, in addition to the hairs on the ninth tergite as given by Marshall and Staley, to be the post-genital plate and the insula. Towards either side of the rounded conical apex of the former structure there arise about 3 longish hairs, and forming more or less a line extending on to the ventral aspect of the plate are some 5-6 minute hairs. On the dorsal surface on either side is a single small hair well back towards the base

of the plate. Examination failed to show any variation in this arrangement as between the two forms that could be held to be distinctive. The hairs arising from the insula in both forms constitute a tuft of rather stout small hairs. Neither in number nor in length was any difference apparent in the two forms, the mean for a number of counts being 8.4 in both cases. The mean number of hairs on the lateral portions of the ninth tergite in the female in a small number counted was 9.0 in *C. pipiens* and 11.0 in the autogenous form, agreeing with Marshall and Staley's finding that the hairs were more numerous in the autogenous form, the actual figures given by these authors being 8.8 for female *C. pipiens* and (varying with one exception from 9.7 to 16) an overall mean for 797 counts of 12.4 for *C. molestus*.

The male hypopygium.—The characters in the two forms were, so far as could be seen, identical, with the possible exception that the dorsal processes of the lateral phallosome plates (mesosome of authors) appeared more rounded

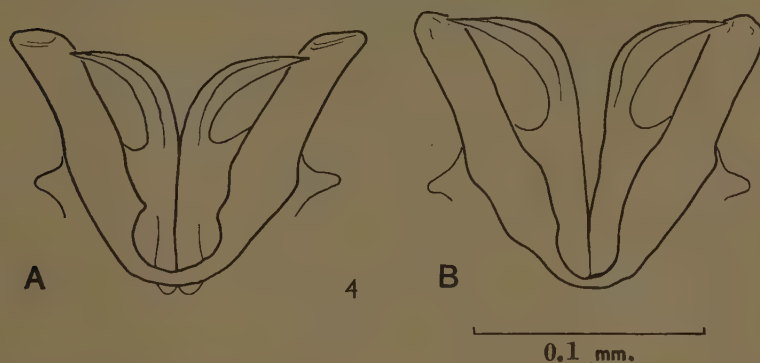


FIG. 4.—Camera lucida drawings of phallosome of A, *C. pipiens* (Cambridge) and B, *C. molestus* (London).

in the autogenous form, and not so flatly cut off as they very conspicuously are in the case of *C. pipiens*. The ventral processes in both cases were similar, their outwardly directed points in every case lying within the limits of the outer margins of the tops of the dorsal processes. A ratio taken by dividing the distance between the outermost extension of the dorsal processes by that between the outer points of the ventral processes in both cases varied from 1.2 to 1.4. Rozeboom in his note on the *Culex pipiens* complex in North America quotes Sundararaman, 1949, as using a ratio of the distance between the tip of the dorsal and ventral process of a side (DV) to that between the two dorsal arms. If the above were put in the form of Rozeboom's ratio the figures would be negative (i.e., -0.07 to -0.14), the points of the ventral arms in every case examined in both forms lying within those of the dorsal arms by a distance of 7 to 14 per cent. of the distance between the dorsal arms. In this connection it may be noted that in *C. fatigans* not only is there a large positive ratio, but the dorsal arms are pointed. The figures given by Marshall and Staley for the number of hairs on the lateral lobes of the ninth tergite

in the male are 8.2 for *C. pipiens* (9310 counts) and 11.6 (mean of 716 counts as given in their tables). In the small number of counts made by me the variation was too great to arrive at any conclusion.

The larva.—The larvae of the two forms are similar in respect to most of

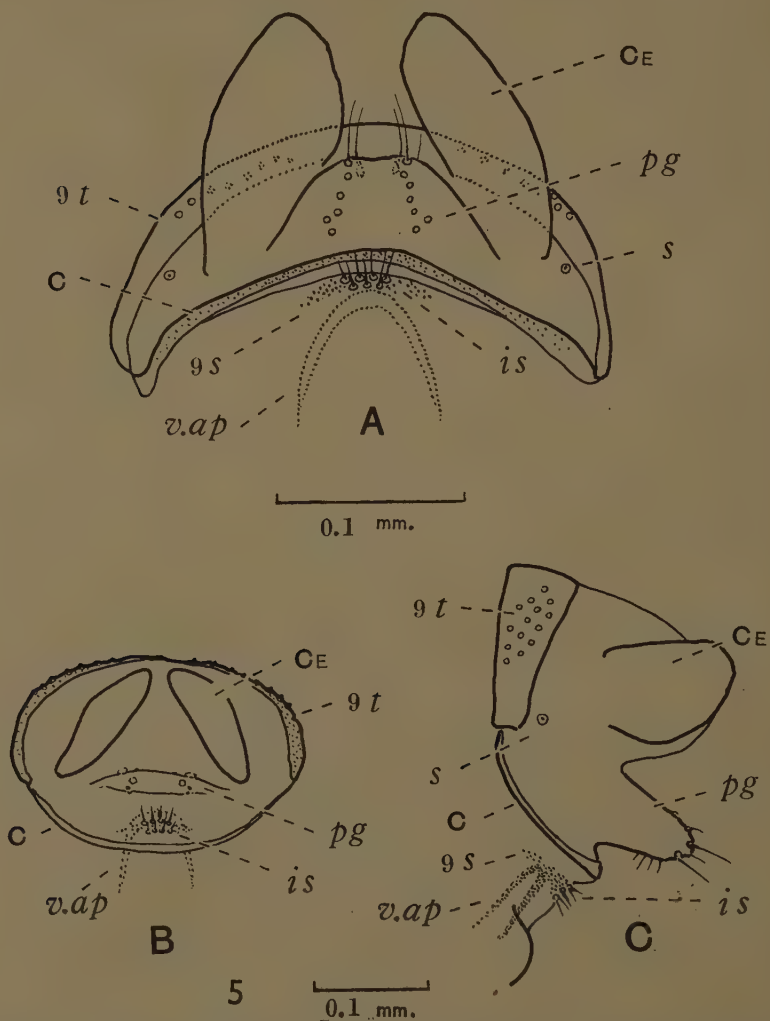


FIG. 5.—A, Female hypopygium of *C. pipiens* (ventral view). B, the same (posterior view). C, Female hypopygium of *C. molestus* (lateral view). *Explanation of lettering.* C, cowl; Ce, cercus; is, insula; pg, post-genital plate; s, sensory pit; v. ap, vaginal apodeme (seen through tissues); 9s, ninth sternite (position of); 9t, ninth tergite.

the differential characters used in identification of this stage, but Marshall and Staley point to a difference in the siphonic index, viz., a mean not exceeding 4.3 for the autogenous form and one of 5 for *C. pipiens*. These authors also found that there was a tendency for a large number of branches of the 4 siphon hairs in the autogenous form. Jobling, 1938, draws attention to the distinction in the shape of the siphon.

There can be no doubt as to the difference in the siphonic index as even the naked eye can detect this, and in the present case measurement of a number of larvae of the two forms gave a figure of 4.25 for the autogenous form and 4.99 for the anautogenous. Equally obvious was the difference in shape, the siphon of *C. pipiens* being very definitely straight in its contours, whilst that of the autogenous form had a more curved outline. Mounted skins even when somewhat compressed showed an easily distinguished more stumpy shape in the autogenous form. The larvae of the two forms as compared above were bred and examined under identical conditions.

The egg and egg-raft.—Marshall and Staley note a difference in measurements of the egg. Roubaud, 1935, has described this micropilar apparatus of the two forms and finds that in the anautogenous form the central area shows a very distinct network with a well-marked border, whilst in the autogenous form the net-work is confused and little apparent. I have already pointed out the great differences in the egg-raft of the three species *C. fatigans*, *C. pipiens* and the autogenous form (Christophers, 1945). It has, however, been pointed out that the characters of the autogenous raft even after a human blood meal are not truly comparable with the egg raft of *C. pipiens* following bird blood. Unfortunately I have not been able to ascertain what the number of eggs may be in the autogenous form after birds' blood or to obtain any certain information in this respect from the literature. I have, however, noted a statement in Tate and Vincent, (1936: 136) which bears upon the question. These authors there speak of the autogenous form as laying egg-rafts without a blood meal of 50–80 eggs plus a blood meal raft given by MacGregor as 150 eggs, i.e., a total of 200–250 eggs, and they go on to say: "This is about equal to the number of eggs laid by a female of the English anautogenous race after one blood meal, although sometimes such females lay very large rafts containing 300 or even 400 eggs." I think it is clear that the authors here mean that the autogenous form lays 50–80 eggs without a blood meal, but that after this if fed on blood they may lay another 150, which is not the same as saying that after a blood meal it lays 200–250 eggs. Dr. Tate also tells me that he feels sure the autogenous form fed on birds' blood does not lay the large egg rafts of the order of 300–400 eggs. It may also be pointed out that *C. fatigans* fed on the birds' blood has been described by me as laying egg-rafts measuring 3 to 4 mm. in length by about 1.3 mm. in greatest breadth and eggs numbering usually 150–200 arranged in 4–5 rows on either side of the middle line, whereas the raft of *C. pipiens* is much larger, measuring as much as 6 mm. in length by 1.8 in greatest breadth and usually 400 eggs arranged in 6–9 rows on either side of the middle line, the middle row being about 40 eggs as against 25 in *C. fatigans* (Christophers, 1947).

Are these two forms distinct species?—That species exists as a concrete fact in nature does not mean that a definition can necessarily be made to cover borderline cases. To define and accept this as one's criterion is against

all the canons of science. In such a case as the present great stress has been laid on the result of crossing, but in insects at least it would not seem that hybridization with fertile offspring necessarily disposes of a specific distinction, otherwise two species such as *Aedes aegypti* and *A. albopictus* must be considered specially identical though they differ obviously in markings and many biological ways. I believe it is correct to say that in zoology the basis of species is morphological, and in practice lies in the ability to identify specimens of the species by some morphological feature or features. It is true that certain difficulties remain, e.g., what degree of morphological distinction is to be recognized as indicating specific and subspecific rank. The answer to this difficulty I think must be that it depends at least in some degree on zoological convenience. An example in the Anophelini are the varietal forms of *A. maculipennis*. Many consider some of these at least to be distinct species for which there are strong reasons, including the results of crossing. But since these forms are not readily distinguished without knowledge of the egg characters it is much more convenient in every way to cover them all by the blanket designation of *A. maculipennis*. On the other hand, a marked tendency in the Anophelini is for varieties on closer study to be shown to be good species, and naming as such is helpful.

In the case of two forms here dealt with numerous small distinctions seem to give a clear indication of specific difference, and once this is granted the profound biological differences in the two forms becomes explicable. Whatever concept may be held as to the nature of a species in the animal kingdom it rests in practice with the systematist to give the appropriate name, and in practice it is ability to identify specimens which is the dominant necessity. Many of the small differences in the two forms which have been pointed out are not very readily usable in identification. Nevertheless there are two characters, one relating to the adult and one to the larva, which are such as systematists are accustomed to use to distinguish species. These are the presence of the dark median scale patches in the autogenous form and their absence or near absence in *C. pipiens*. It is only unfortunate that whilst this character is easily applied to fresh material it is not so readily applied in the dried specimen owing to the curling in of the tergite edges; nevertheless it is usually possible to identify a dry specimen. Obviously in this case also the fact of autogeny and other biological peculiarities of *C. molestus* can be brought in to help. There would seem to be no doubt that a distinct specific name is both justifiable and desirable for the autogenous form. The characteristic siphon of the larva is a quite practical means, too, of identifying the species in the larval stage.

Is the name Culex molestus correctly given to the autogenous form?—Marshall and Staley give very good reasons for their selection of the name *Culex molestus* Forskål. That the autogenous form is not *C. pipiens* Linnaeus as Ficalbi considered the man-biting form to be is clear from the fact given by Marshall and Staley that Linnaeus designated as *Culex pipiens* the mosquito described by Réaumur in his *Mémoires*. Anyone who has seen Réaumur's figure depicting the dark areas on the venter of his species can have no doubt but that it was the anaautogenous, non-man-biting species which Réaumur described. Three possible names relating to man-attacking forms of *C. pipiens* are given by Marshall and Staley, viz., in order of publication: *Culex molestus* Forskål

from the Nile Delta, 1775; *Culex domesticus* Germar, 1817, from Dalmatia, and *C. haematophagus* Ficalbi, 1893, from Italy. Both forms with and without ventral dark spots are stated by these authors to be in the British Museum. Pending further close morphological study of autogenous forms from different countries, and the possibility of more than one species exhibiting autogeny and other characters of *C. molestus*, it seems desirable from a systematic point of view that the name *C. molestus* Forskål should be adopted for the European species. If autogenous forms from other areas are found to show morphological differences from the European form the correct procedure would seem to be to designate these named species or varieties depending upon the nature of the differences. Probably it would be most convenient that they should be regarded as varieties in the sense of subspecies unless very clearly specifically distinct.

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(See Bibliography to section by Lt. Cmdr. Knight.)

CULEX MOLESTUS.

By P. G. SHUTE, M.B.E., F.R.E.S.

(Medical Research Council.)

WHEN I was invited to take part in this discussion I decided to confine my remarks to the bionomics of *Culex molestus* as observed in nature, and to record any salient features which I thought might contribute to our knowledge of this subject.

First a few words about *Culex pipiens*. I am referring to the *Culex* mosquitoes, the larvae of which are so common in artificial water containers everywhere between the months of May and September. In the laboratory I have never succeeded in inducing the females of this species to take a mammalian blood meal, and I have made repeated attempts on various animals including man, monkey, horse, pig, rabbit, dog, and many others. I remember many years ago Professor Leiper asked me if I would collect for him large numbers of *pipiens* which he wished to feed on a dog whose blood was swarming with filaria embryos. Day after day we tried to induce some *pipiens* to feed but not one did so, yet we succeeded quite easily with *Culex fatigans* imported from India.

I have collected numerous blood-gorged *pipiens* from stables, cow-sheds and pig-sties, but always the red cells were nucleated. In July and August chicken-houses swarm with blood-gorged *pipiens* and, as we know, they feed readily on small birds such as canaries and hedge sparrows. On one occasion I noticed a lot of blood-gorged *pipiens* at rest on the leaves and stalks of an ivy creeper against the wall of a house. I dissected a number and found that the red cells were nucleated. A search in the long grass at the root of the ivy revealed a large frog. I took it to the laboratory, put it in a cage with some *Culex pipiens* and the following day most of the mosquitoes had taken a blood meal. Later I tried to induce the same batch to feed on man and rabbit, but without success. From these and other numerous experiments I concluded that either *Culex pipiens* never feed on mammals or that they do so only rarely and under special conditions which were absent in the laboratory.

I was surprised when, in 1923, on being asked to investigate a mosquito nuisance in the heart of London, I found the walls and ceilings of certain bedrooms contained dozens of *Culex* gorged with mammalian blood. Numerous bedrooms in the district were infested, and although a few *Culex* larvae were found in a water-butt, the numbers were out of all proportion to the adults congregated in the bedrooms. Extensive searches for other breeding-grounds were made over a period of two years but none were found. For the next six or seven years no further complaints was received. I well remember the many discussions between Col. James, Dr. F. W. Edwards and myself about this *pipiens* problem, and it was suggested that *pipiens* in the district had become anthropophilic by the force of circumstances, perhaps because access to small birds had become difficult or impossible.

We now come to the time of the 1940 blitz on London when the Underground Railways began to be used for sleeping quarters. The first complaint

of a mosquito nuisance was received from the Chief Medical Officer of the Port of London. Many people had complained of having been bitten at night while resting in the Liverpool Street Underground Station. I visited the station and caught many mosquitoes in the act of biting and satisfied myself that they were *Culex molestus*. Further complaints were made almost daily and covered a wide area of the Underground system, from Clapham Common to Hampstead. Locating the breeding-grounds was not easy, and it was some weeks before these were found to be situated beneath the Underground station platforms, known as inverts. In many cases larvae were extremely numerous even where the depth of the water was only two or three inches. At many points throughout the system there are deep sumps, and in these, too, larvae were numerous. Unfortunately, the water from these inverts was never analysed.

When, in 1941, large static tanks were erected all over London for fire-fighting purposes, it was anticipated that sooner or later these tanks would become infested with *Culex molestus* from the Underground. The tanks were "topped up" at least once a week by the members of the fire brigade and they were taught how to recognize and collect mosquito larvae, and when any were found this was reported and I made an inspection. Although *Culex* larvae were found in hundreds of these tanks, *molestus* were never found. To determine whether the mosquitoes were *pipiens* or *molestus*, use was made of Marshall's description, and also adults were bred in the laboratory to find out whether they were autogenous and stenogamous. We never found *molestus* breeding in these above-ground static water tanks, even though they were numerous in water fifty feet or more below ground level. Rightly or wrongly I attach much importance to this fundamental difference in the bionomics of the two species or varieties.

In 1949 I visited Wembley at the request of the M.O.H. A serious mosquito nuisance had arisen and numerous female adults of *Culex molestus* were found in many bedrooms. Eventually larvae of this species were found breeding in a water-logged basement of a factory which had been built and used as an air-raid shelter during the war. The basement was within a hundred yards of the street, where houses were heavily infested.

Some larvae and adults of this strain of *molestus* were taken to the laboratory and a colony established and this is still being maintained.

We find that about 80 per cent. lay an autogenous batch of eggs, usually between the third and fourth day after emerging. If larvae are reared on a poor diet—exposed distilled water for example—only a small percentage of the female adults lay an autogenous batch of eggs. The number of eggs in a batch which is laid under these circumstances is less than half those laid when the larvae are reared on a good diet.

We have not succeeded in inducing a *molestus* female to lay a second batch of autogenous eggs, but three batches have been laid on a few occasions by adults which have had a blood meal after each laying. (The eggs were laid 24–36 hours after each blood meal.) Occasionally a female of this Wembley strain will take a blood meal on the fifth day after emerging, but the majority do not bite before the seventh to the tenth day. They will feed on rabbits, but not so readily as on man.

If glucose is given before the first batch of eggs is laid it seems to inhibit

egg development and oviposition. Our present colony is being maintained without giving the adults food of any kind.

A male and female *molestus* will mate in a test-tube 3 in. long by $\frac{3}{8}$ in. in diameter, and if the tube is half filled with rain water when the virgin female and the male copulate, eggs are laid, and these, after hatching, will develop to the adult stage over a period of about 18 days at 76° F.

It is my opinion that the *molestus* nuisance in parts of London is quite serious and appears to be on the increase, and that *Culex pipiens*, as we know them, do not feed on mammals. If this is correct, then it seems to me that a clear definition of what is a *pipiens* is of considerable importance; for example, the St. Louis virus of *Equine encephalitis* is stated by American workers to be carried from man to horse by *Culex pipiens*. If, therefore, this species of mosquito never, or only very rarely, feeds on mammals, then the carrier of the virus of *Equine encephalitis* is not *Culex pipiens*.

Species differentiation by morphological characters is, of course, of the greatest value, but it seems to me that where we have two types of varieties of insects behaving quite differently in nature in the same locality, even if, at the time, the two types cannot be separated morphologically, it cannot be taken that they are not separate species. I say at the time, because there are a number of examples where morphological characters between two closely related species have not been found for a long time, even though bionomically they are different. *Anopheles maculipennis* is an example. *A. messeae* and *typicus* hibernate completely, *atroparvus* and *labranchiae* do not. For many years systematists failed to find morphological characters whereby one could separate individuals of the *maculipennis* complex. Eventually it was found that there were minute differences in the construction of the male genitalia and that these differences were constant. Later still it was found that adult individuals of the *A. maculipennis* group could be separated by the shape of the plume scales of the wing. It would not, I think, be claiming too much to say that it was the result of the studies of the bionomics which led to the discovery of the *A. maculipennis* complex, and although it has not yet been universally agreed to raise these "varieties" to species rank, most workers believe that they are true species.

Another example of a species being recognized through its bionomics may be quoted. There are two well-known species of *Culicella* in this country: *C. morsitans* and *C. fumipennis*. Both breed in fresh water in and around woodland areas. Some years ago larvae resembling *morsitans* were found in a brackish ditch in company with *Aedes detritus*, *Aedes flavescens*, *Aedes dorsalis* and *Aedes caspius*. As this was an unusual situation in which to find *morsitans* some were reared to the adult stage and on examination they were found to be a hitherto undescribed species—*Culicella litorea*.

Bionomically *Culex molestus* and *Culex pipiens* are even more widely separated than any of the *A. maculipennis* group, and if, as our present inquiries indicate, *molestus* adults are unable to develop an adipose body and therefore cannot pass the winter as a fertilized insect, the bionomic differences in the two are such that it is difficult to believe that they are not distinct species.

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THE PHLEBOTOMINAE OF THE ETHIOPIAN REGION.¹

By R. KIRK, O.B.E., M.D., and D. J. LEWIS, M.A., F.R.E.S.

(The Stack Medical Research Laboratories, Khartoum, Anglo-Egyptian Sudan.)

Manuscript received 16th March, 1951.

(Read 15th August, 1951)

With 74 Text-figures.

*I have gathered a posy of other men's flowers
and nothing but the thread that binds them is mine
own.*—MICHEL DE MONTAIGNE.

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INTRODUCTION.

DIFFICULTY in the identification of *Phlebotomus* arises from the small size of the insects, and from the fact that in most cases specific characters are found only in the internal structures so that each specimen has to be cleared, dissected under the binocular, and then examined under low and high powers of the microscope before it can be identified. In our experience the greatest difficulty of all arises from the scattered nature of the literature, which is, nevertheless, copious. Sinton (1932, 1933) published illustrated keys for the identification of males and females which form a useful starting-point as regards the Indian species. In our studies of the sandflies of the Sudan, extending now over twelve years, we were at first much impeded by the fact that no similar guide was available for the Ethiopian species. We found that the only way to avoid confusion was to copy from the various journals descriptions and figures of each species, and to bind these abstracts together in a single file. By so doing we were able to collect in convenient form an up-to-date account of all the species which had been found in the Sudan and adjacent countries. From this

it was possible to construct keys and diagnostic tables which proved of great assistance in the identification of specimens.

We have from time to time published some of those keys and diagnostic tables for the Ethiopian species, including additions and revisions which have been made necessary by increases in knowledge in recent years. The suggestion that these papers should be collected, and expanded into a comprehensive, up-to-date monograph on the Ethiopian species of *Phlebotomus* was made first of all by Dr. P. C. C. Garnham, of the London School of Hygiene and Tropical Medicine. Other authorities with whom we discussed Dr. Garnham's suggestion considered that such a work might be very useful at the present time, as there is evidence of increasing interest in this important genus of biting insects, especially in Africa.

The present work is the outcome of Dr. Garnham's suggestion, and is presented in the hope that other workers in Africa may find it at least a useful guide to the copious and scattered literature on the subject. No one could be more conscious than the authors of the defects and deficiencies of this work, which deals with matters of classification and synonymy on which opinion is divided at present. Some of the most difficult points have, in fact, been laid before the International Commission on Zoological Nomenclature for their final ruling, which may ultimately prove to be different from that anticipated in this work.

It is a very great pleasure to acknowledge the kind assistance of others who have helped us in this work. First of all to the late Emeritus Professor R. Newstead, who even in his retirement spared no pains to ensure that we were provided with reprints and information on the earliest work on *Phlebotomus*. Thanks are also due to Dr. L. Parrot, of the Institut Pasteur d'Algérie, who has examined many of our specimens and generously given us the benefit of his advice and experience on many points during the course of this work; to Professor P. A. Buxton for his interest and encouragement and for access to collections in the London School of Hygiene and Tropical Medicine; to the Keeper of Entomology for access to collections in the British Museum (Natural History), and to Mr. P. Freeman and Mr. H. Oldroyd for their advice and assistance; to Professor R. M. Gordon and Dr. D. S. Bertram for access to collections in the Liverpool School of Tropical Medicine; to Dr. B. De Meillon for information on South African species; and to Mr. H. D. Fowler for chromatographic analyses of diverticulum contents of *P. papatasi*.

We also acknowledge our indebtedness to the following journals for permission to reproduce figures of *Phlebotomus* as indicated in the descriptions of the figures: *Annales de Parasitologie, Humaine et Comparée*; *Annals of Tropical Medicine and Parasitology*; *Archives de l'Institut Pasteur d'Algérie*; *Bulletin of Entomological Research*; *Indian Journal of Medical Research*; *Journal of the Entomological Society of Southern Africa*; and the *Proceedings of the Royal Entomological Society of London*.

I. LIFE HISTORY, BIONOMICS, DISTRIBUTION, IMPORTANCE AND CONTROL.

LIFE HISTORY.

Egg. The egg of *Phlebotomus* is an elongate torpedo-shaped body about 0.4 mm. in length with rounded ends. It is pale in colour when first laid, but soon becomes dark brown or black. The surface shows a peculiar sculpturing

due to the impressions of the cells of the egg follicle, and the pattern varies in different species. The female lays 20-40 eggs in a batch, depositing them on the sides of holes and cracks in the ground and similar places where the required darkness, humidity and shelter exist. The incubation period is approximately a week.

Larva. There are four larval stages. The first larva hatches from the egg by breaking through the shell with the aid of the egg breaker, a specialized chitinous structure on the front of the head. Hatching is completed in a few minutes, and the long caudal bristles, which are at first folded back, then straighten out. The larva has a well-developed head with characteristic bristles and mandibulate mouthparts, but eyes are lacking. The antennae are small and rudimentary. The epicranial suture is well developed, with the small, dark, pointed egg breaker between its two anterior limbs. The three thoracic segments are distinct. There are ten abdominal segments, the first seven of which are readily recognizable by the ventral pseudopod on each. On the dorso-lateral margin of the eighth segment there is a small spiracle, situated on a chitinous tubercle (*metapneustic* larva). The ninth segment bears on a chitinous plate a pair of characteristic, long, caudal bristles which are held erect as the larva crawls about. There are two unequal bristles at the sides of the tenth segment, and the eleventh segment is represented by a pair of membranous pads between which the anal opening lies. The body segments bear characteristic bristles with globular swellings at their apices. The structure and arrangement of these bristles differ in different species.

When the first larva moults it loses its egg breaker, and this structure, being no longer required, does not appear in the second and succeeding stages. In these stages an additional pair of metathoracic spiracles are developed (*amphi-pneustic* larva) and a second pair of caudal bristles.

The larva of *Phlebotomus* crawls about slowly like a small caterpillar, shams death if disturbed, and is extremely difficult to detect in nature, its colour harmonizing with its surroundings. The larvae feed on organic matter, such as dead leaves, excreta, dead bodies of insects, vegetable debris, etc. Parrot (1932) has shown that they can be reared on dead leaves alone without any animal matter, and this is probably their principal food in nature (Wanson, 1942). In some species the larva can withstand a certain amount of desiccation and freezing, but as they usually live some distance below the surface of the soil they are largely protected from such adverse climatic conditions as heat and desiccation in the Sudan or intense cold in Northern China. The period of diapause by which some species hibernate, and others possibly aestivate, occurs in the fourth larval stage.

Pupa. When fully grown the fourth larva stops feeding and, selecting a suitable spot, becomes motionless with its head and most of the body raised in a very characteristic erect attitude. At this stage the larva may have an opaque swollen appearance due to the formation of the pupa inside the larval skin. The pupa by its movements splits the skin along the dorsal surface of the thorax and then worms its way out through the rent, the head of the larval skin passing along its ventral surface. The pupa of *Phlebotomus* has a very characteristic appearance, as the last larval skin is always attached to the end of it and the four caudal bristles, even if broken off short, can always be made out at the end of the larval skin. There is no other nematoceros larva which

has similar bristles. The developing imago can usually be made out through the thin skin of the pupa (*pupa oblecta*), and when seen from the front has been described as resembling the head of a ram in miniature, the antennae of the developing fly representing the horns of the ram. The imago emerges through its pupal case by a straight cut in the dorsal surface (*orthorrhapha*). The dorsal surface of the thorax protrudes through the rent, which then allows the rest of the thorax and the head to emerge; lastly the legs and wings are drawn out. Emergence is completed within a few minutes, and then rotation of the terminalia through 180 degrees occurs. The pupal skin left behind is clearly recognizable as that of *Phlebotomus*.

Time occupied by the different stages. The time occupied by the complete cycle varies with temperature and season. At Matadi in the Belgian Congo Wanson (1942) found that it varied between 51 and 56 days in *P. schwetzi*, *P. africanus* and *P. squamipleuris*. In North Africa Parrot (1932) observed periods about three times this duration in the case of *P. papatasi*. These periods do not include any period of diapause. In places where there is a well-marked sandfly season the life cycle may be greatly lengthened by a period of diapause in those broods which hatch out at the end of one season and reach maturity at the beginning of the next one. Some observations on the duration of the different stages in the life cycle are given below.

The period of incubation of the egg is about a week at 28° C. Patton gives up to 12 days in North China.

The duration of the larval stage varies with temperature and season, but is between 35 and 40 days at 28° C., excluding diapause.

The duration of life of the adult varies considerably. Unfed females and males die about the fourth day after emergence, the females having laid no eggs. In captivity females often die during or immediately after egg-laying, but in nature many survive and may live up to 40 days or longer, laying eggs several times provided blood meals are obtained at suitable intervals. A single blood meal suffices for the maturation of ova provided it is large enough and the external temperature sufficiently high. Copulation may occur either before or after the female gorges on a blood meal. Once gorged the female does not fly more than a few feet from the place where she has fed, but seeks the nearest place of refuge which offers suitable conditions of darkness, still air and humidity. Digestion of the blood meal is completed in about 72 hours at 28° C. and the eggs are laid 30–36 hours later.

Breeding places. Sandflies breed in such places as dark and damp cellars, out-houses, caves, dug-outs, piles of rubble, stones, bricks and tiles, crevices in damp stone walls, drains and the banks of streams, cracks and fissures in the soil and animal burrows. In arid semi-desert conditions it has been shown that soil cracks and animal burrows may provide suitable microclimatic conditions of temperature and humidity for sandfly breeding throughout the year. Moist organic matter is essential as well as shelter and darkness, but too much moisture drowns the larvae, and it may be accepted that material from a possible breeding place is too damp if it adheres to the fingers and does not just fall off when rubbed gently between them. Larvae have been found at varying depths in the soil, e.g., by King (1914) in the Sudan and Hindle (Patton and Hindle, 1928) in China. In order to detect them large quantities of soil may have to be examined. This can be done by washing it through sieves of

decreasing size down to 40 strands to the linear inch, and finally through muslin, after which the larvae can be floated off in a concentrated solution of salt in water, or by various modifications of this technique which have been suggested.

In the arid Northern Sudan animal burrows and soil fissures are believed to be the main breeding places of sandflies, cracks in the walls of houses and other situations above ground being probably too dry for larvae except during a short period of the year. The soil fissures are often automatically filled or covered by irrigation, seasonal rains, or the trampling of people or animals. In the Sudan it has often been noticed that houses on the periphery of a town near the untrodden cotton soil are more infested by *P. papatasi* than those in its centre. This has been observed also in more equable climates, where it is attributed to the greater abundance of vegetation suitable for the nutrition of larvae at the periphery of towns.

BIONOMICS OF ADULT.

The adult *Phlebotomus* is a very characteristic insect when seen alive—a small hairy midge with large eyes, long legs and hairy pointed wings held at an angle of 45 degrees. In the male the terminalia are generally conspicuous at the end of the abdomen. The colour varies from light yellow to dark grey, but neither colour nor size can be used to differentiate species. The male and unfed female can readily pass through the mesh of an ordinary mosquito net.

The optimum physical conditions for sandflies are still air, darkness, a constant temperature of approximately 28° C. and high relative humidity (approximately saturation). They are delicate insects, and many features of their bionomics depend on the fact that they do not readily withstand much variation from those optimum conditions, especially as regards temperature and relative humidity. Unless conditions are optimal the females of some species refuse to feed and die of starvation. Theodor (1936) has shown that at 30° C. and a relative humidity of 40 per cent. the mean length of life of fed female *P. papatasi* was 3.5 days, while the thermal death point in a 1-hour exposure was 41° C. Condensation of water vapour from the atmosphere may also be harmful as they readily become entangled and drowned in the drops of water thus formed.

Seasonal prevalence. In most places where sandflies are prevalent they exhibit a more or less marked seasonal variation in numbers. In some regions there is a well-defined sandfly season, the prevalence of the flies being restricted to a few months of the year. The seasonal variation in numbers is closely correlated with meteorological conditions, and thus varies in different areas according to the climate. The dominating factors are temperature, humidity, rainfall, insolation and wind, especially the first three. In most places sandflies disappear during the heavy rains. This is so in the Sudan (Kirk and Lewis, 1940), Abyssinia (Martin, 1938) and the Belgian Congo (Wanson, 1942), and in these regions the greatest prevalence occurs just before the rains and, later, shortly after them.

Diurnal prevalence. Adler and Theodor (1931) have drawn attention to the diurnal periodicity of certain species in the Mediterranean zone, by which it is possible to predict almost to an hour when members of a particular species will appear inside houses. In the Sudan a similar diurnal periodicity has been

observed in *P. papatasi* and *P. freetownensis* var. *magnus*, and in the Congo Wanson (1942) has noted that *P. africanus* and *P. schwetzi* were prominent in day-time catches, *P. durenii* and *P. squamipleuris* in night-time catches.

Range of flight. Sandflies are absolutely silent in their movements. They have a characteristic way of flying in short hops, and if disturbed they move in this way very rapidly. They may occasionally fly surprisingly long distances for such delicate insects, but the range of flight is normally very limited, probably less than 300 yards. Dodds-Price and Rogers (1914) found that removal of coolie lines to a new site 300 yards away was sufficient to cut short the occurrence of new cases of kala azar. Rarely they may travel further with the assistance of winds and air currents. But winds and air currents have a markedly deterrent effect on sandflies and they do not readily venture out into them. Sandflies do not fly high; hence although plentiful at ground level they are usually much rarer in the upper stories of houses but not always, and they have been known to enter bedrooms 50 feet above ground level, probably from high breeding—or resting—places.

Resting places. Sandflies are mainly nocturnal and disappear during the day-time when they may be found resting in dark corners, especially where moisture is present, behind clothes, cupboards, pictures, etc., in the interior of rubble and stone walls, in crevices in trees, drains, caves, dug-outs, and the banks of streams, amongst heaps of damp stones, bricks, tiles, clods of earth; also in animal burrows and in cracks and fissures in the soil. *P. gigas* and *P. mirabilis* occur typically in caves. *P. adleri*, *P. affinis* and *P. christophersi* var. *calcaratus* have been found chiefly on or near rocky areas. *P. squamipleuris*, though ubiquitous, is associated with damp conditions, e.g., the edges of pools and banks of rivers; it is attracted to artificial light more than other species, and hence often comes into lighted mosquito-proofed verandahs.

Kirk and Lewis (1947) concluded that the survival of sandflies in some arid areas is due in large measure to their exploitation of a vast subterranean environment, consisting of animal burrows and cracks in the soil in which equable conditions of temperature (27° C.) and relative humidity (approximately 100 per cent.) exist in spite of wide fluctuations above ground. From this subterranean environment they emerge in search of food only after darkness, when the temperature falls and the relative humidity in consequence rises, thus providing suitable climatic conditions for them. Many no doubt find nourishment in animal burrows and in the soil fissures which are inhabited by scorpions, lizards, bats, and other insects besides sandflies. The obliteration of the soil fissures annually by the rains is probably an important factor influencing the seasonal prevalence of *Phlebotomus*.

Many authorities differentiate "wild" and "domestic" species of *Phlebotomus*, the latter being those found frequently in human dwellings, while the former are found mainly in outdoor situations and rarely if ever enter houses. Wanson (1942) considers the terms wild and domestic are inappropriate, since the domestic species can usually be found out of doors with little difficulty and their relative abundance in houses is merely the expression of a preferential food tropism which leads them to seek resting places near the host animal of choice (man). In Russia Petrischeva (1932, 1935) noted that when previously unoccupied regions were occupied by man various species of *Phlebotomus* (e.g., *P. minutus*, *P. caucasicus* *P. sergenti*, which had previously been

recorded in these regions from burrows of rodents and land tortoises) acquired domestic habits, finding conditions favourable for development, shelter and food in association with man and domestic animals.

Feeding habits. In spite of the minute size of *Phlebotomus* their bites may cause severe irritation. They are often described as crepuscular in their biting habits, but they are mainly nocturnal, although they will readily bite in the day-time in dark rooms, latrines and similar places. It is possible that, as in the case of mosquitoes, each species has its peak hour of biting during the night, but there is little information on this subject. Human beings are generally bitten on the face, hands, arms, ankles and legs, the parts of the body most exposed when sitting out in the verandahs of tropical houses or sleeping without adequate protection.

Only the females suck blood, but little is known about the biting habits of most species. Parrott (1934) considered that species with a well-developed buccal armature (*Prophlebotomus*) are habitual parasites of cold-blooded animals and rarely if ever bite man or warm-blooded animals, while those with unarmed buccal cavity (*Phlebotomus*) are habitual parasites of man and warm-blooded animals. In general this may be so, but there are some exceptions and many species about which no data are available. Our present information about the biting habits of sandflies in the Ethiopian Region may be summarized as follows.

P. papatasi bites man voraciously indoors and out of doors; it will bite also dogs, monkeys and various rodents. *P. orientalis* bites man very readily. *P. martini* and *P. longipes* are recorded as biting man in Abyssinia by Martin, who records also dogs, rabbits, guinea-pigs, fowls and pigeons for the latter species. *P. clydei* bites man in and out of doors, but is principally an outdoor species; it will bite also monkeys, ground squirrels, hamsters and dogs. *P. squamipleuris* has been observed biting frogs (Lewis and Kirk, 1950), and Wanson (1942) has identified lizard's blood in its gut by precipitin tests. *P. antennatus* var. *signatipennis* and *cinctus* commonly bite gecko lizards and seldom or never bite man. *P. freetownensis* var. *magnus* (= *P. africanus*) bites man rarely: Wanson's precipitin tests showed that it bit man and lizards. Sinton (1932) records *P. bedfordi* var. *congolensis* as biting man in Kenya. It would be interesting if the Kenya observations could be repeated, as the collection of *P. bedfordi* var. *congolensis* received by Sinton and reported as biting appears to have included males. Theodor (1931) and Wanson (1942) record *P. schwetzi* as biting man in the Belgian Congo, and we have received specimens taken on man from Mombasa. This species will also bite monkeys, fowls, rabbits, bats and lizards. Wanson (1942) records *P. mirabilis* and *P. gigas* as feeding on bats, and *P. durenii*, *P. collarti* and *P. wansoni* on lizards.

The host range of many of the species mentioned above is probably wider than is indicated, but only authentic records are given. Little is known about the feeding habits of the other species or of the males of any of the species. Some authorities believe that the males never feed although they are provided with piercing and sucking mouthparts as in the females. It has often been suspected that in the absence of suitable animal hosts sandflies suck the juices of plants. Smith, Halder and Ahmed (1940) found it was possible to maintain them in the laboratory by allowing them to feed on raisins, which they did by piercing the skin with the proboscis and sucking the juices. None of the Ethio-

pian species have been observed to feed on plants in nature, but it has often been suspected that certain Neotropical species do so, and the remarkable proboscis infections with *Bartonella*-like organisms described by Hertig (1938) were considered to have been derived from other sources than blood meals. In some uninhabited, semi-desert areas of the Sudan animal hosts appear scarce, yet sandflies may emerge at night in such large numbers as to suggest that most of them must die without ever having a meal unless they have some alternative food supply. The contents of the oesophageal diverticula of seven female *P. papatasi* caught at Wad Medani were examined by chromatographic analysis by Mr. H. D. Fowler. He found that they all contained glucose and sucrose and one contained fructose showing that they had fed on plant juices.

DISTRIBUTION.

There are many parts of the Ethiopian Region in which nothing is known of the *Phlebotomus* fauna. Where surveys have been made many of the records must be discarded because the species concerned have been subdivided, and the same thing may happen again in species which show much variation. Furthermore the Ethiopian fauna cannot be adequately compared with those of other zoogeographical regions until these have been comprehensively described. Nevertheless, enough is known of the Ethiopian fauna to warrant certain comments and conclusions.

The known distribution of *Phlebotomus* in the Ethiopian faunal areas was summarized by Lewis and Kirk (1949), since when three new forms have been described and the status of several others altered. The distribution of the species in the Anglo-Egyptian Sudan was mapped by Lewis and Kirk (1951). In the present work distribution lists of each species have been confined to countries owing to the difficulty of verifying many of the individual records. In the following general notes on distribution, numbers are approximate in view of the constant changes in our knowledge of the species.

The zoogeographical areas mentioned are those of Chapin, which are based on the distribution of birds and have been discussed by Edwards (1941) in relation to the distribution of mosquitoes. *P. hirtus* is included as an Ethiopian species because it occurs in the Ahaggar with other Ethiopian species very near the border of the Region.

The known Ethiopian *Phlebotomus* fauna comprises 58 species and 24 varieties, which are about half of the entire Old World fauna. Very few are common to the neighbouring Palaearctic or Oriental Regions. They are *P. papatasi*, *P. alexandri*, *P. clydei*, *P. christophersi*, *P. antennatus* var. *signatipennis*, *P. babu* (Seychelles), *P. freetownensis* var. *eremitis* and *P. squamipleuris*. Apart from the last-named most occur in the north of the Region. Several other forms are closely allied to some of those species, such as *P. roubaudi* and *P. papatasi* var. *bergeroti*.

Faunal areas. Within the Ethiopian Region one can already see the characteristics of the *Phlebotomus* faunas of several of Chapin's Provinces.

In the Guinean Forest Province 15 species and four varieties have been found, six of which, *P. bedfordi* var. *medius*, *P. lumsdeni*, *P. crosarai*, *P. free-townensis*, *P. renauxi* and *P. richardi*, appear to be restricted to the Province. *P. bedfordi* var. *firmatus*, *P. schoutedeni*, *P. simillimus*, *P. freetownensis* var.

niger, *P. ingrami*, *P. collarti*, *P. decipiens* and *P. duren*i form a group which is evidently centred on this Province. Of the remaining five forms three are widely distributed in the Region. No species of *Sintonius* has been found in the Guinean Forest Province.

In the Guinean Savanna Province 22 species and six varieties are known of which seven species have not yet been found in other areas—*P. burtoni*, *P. gigas*, *P. hunti*, *P. kirki*, *P. mirabilis*, *P. pastorianus* and *P. yvonnae*.

There are no certain records from the Humid Montane Province.

In the Sudanese Province 27 species and 12 varieties are known, including *P. affinis* var. *vorax* which was inadvertently omitted from Lewis and Kirk's list. The total number is half that for the whole Region, this rather arid Province containing many more species than any other. The distribution of *Phlebotomus* in this Province shows marked differences from that of mosquitoes which was discussed by Edwards (1941). The distribution of mosquitoes shows no clear distinction between the Guinean Savanna and Sudanese Provinces, but within the latter indicates a well-marked division between the Sudanese Arid and Sudanese Savanna Districts. In the distribution of *Phlebotomus* there is a marked distinction between the Guinean Savanna and Sudanese Provinces and very little between the Sudanese Arid and Savanna Districts. Unlike the mosquitoes *Phlebotomus* is well represented in the Sudanese Arid, although in both groups of insects there are several exotic forms.

The North East African Province supports 14 species and eight varieties, *P. heischi*, *P. notatus* and *P. wurtzi* being confined to it. *P. subtilis*, closely allied to the Palaearctic *P. tiberradis*, is very common on the coast and also occurs inland.

In the Eastern and Southern Province 15 species and eight varieties are known of which *P. katangensis*, *P. rossi*, *P. caffrarius*, *P. meilloni*, *P. meilloni* var. *suberectus*, *P. thomsoni*, *P. transvaalensis*, *P. yusafi*, *P. schwetzi* var. *nigricans*, *P. freetownensis* var. *meridionalis* appear to be restricted to this Province.

Discontinuity in distribution is shown by some species. *P. alexandri*, which covers a large area in the Palaearctic Region, has been found only in one Ethiopian locality, 850 miles from the border, despite collecting in much of the intervening area. The Oriental *P. christophersi* occurs in the southern Sudan, separated from the Oriental Region by a tract in which its variety *calcaratus* occurs. Some species are closely allied to others occurring in distant areas, *P. martini* of the Abyssinian Highland District and Sudan being almost identical with *P. katangensis* of the Rhodesian Highland District, and *P. clydei* of the Sudanese Province being closely allied to *P. meilloni* of the Transvaal.

Notes on species and varieties. The species of *Sintonius* occur chiefly in the drier parts of the Region, but other subgenera are more widespread.

The forms of *Phlebotomus* which are known to be widely distributed and abundant over large areas are *P. schwetzi*, *P. squamipleuris*, *P. bedfordi* var. *congolensis*, *P. papatasi*, *P. clydei*, and the various varieties of *P. freetownensis* and *P. antennatus*.

There is a tendency for large dark-coloured species or varieties of *Phlebotomus* to occur in the more humid areas, such as *P. simillimus*, *P. freetownensis* var. *niger*, *P. schwetzi* var. *nigricans* and central African *P. bedfordi* var. *congo-*

lensis. Pale *Phlebotomus* in dry country are seen for example in *P. affinis* var. *vorax* from the Nuba Mountains.

The ecological requirements of the Ethiopian species are little known, but the distribution of some of the species gives an indication of them. *P. gigas* has only been found in caves. *P. christophersi* and its variety *calcaratus* have always been found on or near rocky hills, and *P. clydei* flourishes mainly in arid country with numerous fissures caused by dry season cracking of clay. *P. subtilis* is particularly common in coastal localities, and *P. squamipleuris* is often found in damp situations.

Chapin's 17 zoogeographical districts are named and grouped as follows, and the species of *Phlebotomus* known to occur in each district are shown in the accompanying table:

I. WEST AFRICAN SUBREGION.

A. Guinean Forest Province.

1. Upper Guinea Forest District.
2. Lower Guinea Forest District.

B. Guinean Savanna Province.

3. Upper Guinea Savanna District.
4. Ubangi-Uelle Savanna District.
5. Southern Congo Savanna District.
6. Uganda-Unyoro Savanna District.

II. EAST AND SOUTH AFRICAN SUBREGION.

C. Humid Montane Province.

7. Cameroon Montane District.
8. Eastern Montane District.

D. Sudanese Province.

9. Sudanese Arid District.
10. Sudanese Savanna District.

E. North-East African Province.

11. Abyssinian Highland District.
12. Somali Arid District.

F. Eastern and Southern Province.

13. East African Highland District.
14. Rhodesian Highland District.
15. East African Lowland District.
16. South-East Veldt District.
17. South West Arid District.

RELATION TO DISEASE.

Irritation of bites.—The reaction to sandfly bites has been the subject of considerable attention. Newcomers to a sandfly country often develop a skin eruption of urticarial type. Face, arms and legs are covered with intensely irritating papules, some of which develop into blisters filled with clear or sometimes haemorrhagic fluid. They may become septic through scratching so that the original clinical picture is obscured. In Palestine, where the condition is known locally as "harara," Dostrowsky (1925) concluded on the basis of clinical observation that it is "nothing else than the reaction to sandfly bites" in newcomers to the sandfly country. Experimental work shows (Theodor, 1935) that a process of sensitization to the bites takes place in a relatively short time and is followed later by a slow process of desensitization.

East and South African Subregion.																				
West African Subregion.																				
Guinea, Forest.						Guinea, Savanna		Montane.			Sudanese.			North-East African.			Eastern and Southern.			
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17				
<i>P. adleri</i>	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.				
<i>P. affinis</i>	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.				
<i>P. a. var. vorax</i>	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.				
<i>P. alexandri</i>	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.				
<i>P. antennatus</i>	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.				
<i>P. a. var. cinctus</i>	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.				
<i>P. a. var. dubius</i>	.	+	+	.	.	.	.	+	+	+	.	.	.	.	.	.				
<i>P. a. var. occidentalis</i>	.	.	+	.	.	.	.	+	+	+	+	.	.	.	.	.				
<i>P. a. var. signatipennis</i>	.	+	+	+	.	.	.	+	+	+	+	+	.	.	.	.				
<i>P. aretusi</i>	.	.	+	+	.	.	.	+	+	+	+	+	.	.	.	.				
<i>P. bedfordi</i>	.	.	+	+	.	.	.	+	+	+	+	+	+	.	.	.				
<i>P. b. var. congolensis</i>	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.				
<i>P. b. var. firmatus</i>	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.				
<i>P. b. var. medius</i>	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. babu</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. buxtoni</i>	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.				
<i>P. caffericus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. christophersi</i>	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.				
<i>P. c. var. calcaratus</i>	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.				
<i>P. clydei</i>	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.				
<i>P. collarti</i>	.	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.				
<i>P. coulandi</i>	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.				
<i>P. crosacii</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. decipiens</i>	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.				
<i>P. durenti</i>	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. frederounensis</i>	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
<i>P. f. var. ater</i>	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.				
<i>P. f. var. eremitis</i>	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.				
<i>P. f. var. longior</i>	.	.	.	.	.	.	.	.	+	+	+	.	.	+	+	.				
<i>P. f. var. magnus</i>	.	+	+	+	+	.	.	.	+	+	+	.	.	.	.	.				
<i>P. f. var. meridianus</i>	.	+	+	+	+	.	.	.	+	+	+	.	.	.	.	.				
<i>P. f. var. niger</i>	.	+	+	+	+	.	.	.	+	+	+	.	.	.	.	.				
<i>P. f. var. sudanicus</i>	.	.	.	+	+	.	.	.	+	+	+	.	.	+	.	.				
<i>P. gigas</i>	.	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.				
<i>P. guiraudi</i>	.	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.				
<i>P. heischei</i>	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.				

Theodor concludes that the "harara" of Palestine represents the reaction to sandfly bites at the height of the sensitization process.

Oriental sore. The possibility that leishmaniasis might be transmitted by *Phlebotomus* was first envisaged by the Sergents (1905) and Pressat (1905). In 1911 Wenyon observed leptomonads in wild-caught sandflies in Aleppo, and considered the possibility that these might be developmental forms of *L. tropica*. In 1921 the Sergents, Parrot, Donatien and Bequet produced a typical oriental sore in a man in Algiers by inoculation of crushed sandflies collected in Biskra, a well-known endemic centre of the disease. After much unsuccessful experimental work it was finally shown by Adler and Ber (1941) that *P. papatasi* can transmit oriental sore by the bite from one human being to another.

Kala azar. Following the work of the Sergents and their colleagues in Algiers, Sinton found that the distribution of kala azar in India corresponded roughly with that of *P. argentipes*. As a result of this observation Knowles, Napier and Smith (1925) fed specimens of *P. argentipes* on cases of kala azar, and found that the parasites underwent multiplication and development in this species. During the following twenty years evidence was accumulated to show that the incidence of leishmaniasis in various endemic regions is as intimately associated with the distribution of specific sandflies as is that of malaria with anopheline mosquitoes, but all attempts to transmit kala azar by the bite of the sandfly were unsuccessful. Finally Swaminath, Shortt and Anderson (1942) using the technique of feeding the flies on fruit juices devised by Smith Halder and Ahmed (1940), were able to show that *P. argentipes* can transmit kala azar from one human being to another by the bite.

General remarks on Phlebotomus and leishmaniasis. The specific sandfly vector is different in the different endemic areas, but may be recognized by the facts: (1) that its distribution agrees with that of leishmaniasis, (2) that it is comparatively easy to infect with the local leishmania; (3) that the infection in the sandfly extends forwards into the head (pharynx and prepharynx); (4) that the infection does not die out, but persists for the remainder of the life of the sandfly; and (5) the sandfly is sufficiently prevalent to maintain the cycle of infection. On these criteria *P. papatasi* can be regarded as the vector of oriental sore in Palestine, *P. sergenti* in India and Bagdad. Parrot (1943) names *P. roubaudi* as the probable vector of oriental sore in the Niger basin. *P. argentipes* is the vector of kala azar in India, *P. chinensis* in China, *P. perniciosus* in the western Mediterranean, *P. major* in Crete, and *P. orientalis* in the North-Eastern Sudan. In the Old World in general kala azar is transmitted by species of the *major* group, oriental sore by species of the *sergenti* and *papatasi* groups. We have suspected that *P. clydei*, which is outside these groups, may act as a vector in some parts of Africa, but feeding experiments (admittedly on a small scale) have not borne out this supposition. In the New World leishmaniasis is probably transmitted by several species of Neotropical sandflies. Much interesting work still remains to be done in identifying and mapping the distribution of the vectors of leishmaniasis in Africa and in the New World.

In Russia it has been shown that oriental sore is essentially a zoonosis among burrowing rodents transmitted by *Phlebotomus* spp. Man may become infected by breaking accidentally into this sandfly-rodent-sandfly cycle. The infection may be taken by an infected human being into urban areas and

thereafter transmitted from man to man by sandflies without the intervention of rodent reservoirs, as a result of which it alters its character in certain respects and becomes more specifically fixed for human beings. It is possible that other forms of human leishmaniasis will ultimately be shown to have a similar origin from some reservoir host.

Much interest attaches to the innumerable failures to infect man and animals by the bites of infected sandflies until, after the technique of feeding these insects on fruit juices was evolved, it was found that intense infection developed in the flies and transmission by the bite could be effected with comparative ease. At present it is impossible to say whether anything comparable to this takes place in nature; but it has been suggested that those instances in which the distribution of the vector is known to be wider than that of the infection might be explained by the limitation of the infection to areas in which the flies were able to feed on fruit juices which stimulated the development of the parasite. These suggestions are, however, purely speculative.

Sandfly fever. Doerr, Franz and Taussing (1909) in Herzgovina proved that this disease is transmitted by *P. papatasi*, and other workers have since confirmed this observation. The distribution and seasonal prevalence of *P. papatasi* corresponds almost exactly with that of sandfly fever. The causal agent is a filterable virus, and the blood is infective to sandflies for 24 hours before the onset of symptoms and 24 hours after it. The female *P. papatasi* becomes infective from seven to ten days after feeding on a patient with sandfly fever during the period in which the virus is circulating in the blood. Whittingham and Rook (1923) claim to have shown that the infection is transmitted hereditarily to the progeny of an infected *P. papatasi*.

Other diseases. The diseases known as oroya fever and verruga peruana, which appear to be limited in distribution to certain narrow valleys in the Andes are transmitted by *Phlebotomus* (Hertig, 1938).

In 1948 Smithburn *et al.* produced yellow fever in a rhesus monkey by inoculating an emulsion made from crushed wild-caught *Phlebotomus* spp. in Uganda. The origin of the virus in the *Phlebotomus* is unknown, and it is impossible to say whether this observation indicates merely an accidental infection or the possibility that *Phlebotomus* may play some part in the natural history of yellow fever. The possibility that in addition to sandfly fever other viruses which circulate in the blood may survive and multiply in *Phlebotomus* is an interesting one on which little experimental work has been done.

It has been shown (Yao, Wu and Sun, 1938) that the embryos of *W. bancrofti* will undergo development in *Phlebotomus* spp., but these insects have never been seriously suspected as vectors of filariasis.

CONTROL.

Control of breeding. The range of flight of the sandfly is comparatively small, and the eradication of breeding places within 300 yards of houses, camps, barracks, etc., will do much to reduce the numbers of these insects. It is generally recommended that the following points receive attention:

- (1) Removal of all rubbish, especially heaps of rubble and other debris of building operations.

- (2) Grouting, facing and pointing the walls of buildings, etc., in which crevices have appeared likely to provide suitable breeding-places for sandflies.
- (3) Levelling the ground by rolling, filling up holes and cracks, rendering the surface impermeable with cement, tar, asphalt or similar material.
- (4) The elimination of cracks and crevices in the banks of streams, drains, etc., by smoothing off the surface or lining with cement or concrete.

Destruction of adults. As much natural lighting as possible should be provided, and ventilation and air movement should be satisfactory. Spraying with "fit" and similar insecticides is useful as a temporary measure. The use of D.D.T. residual spray in houses is extremely effective and persistent in its action. Special attention should be paid to doors, windows, ventilators and other routes by which the flies can enter from outside. By the use of D.D.T. or gammexane it should be possible to eliminate the sandfly nuisance from houses. Hertig and Fisher (1945) have reported very favourable results on the control of sandflies with D.D.T. in Palestine. Reports from Peru by Hertig and Fairchild (1948) are equally favourable as regards the control of *Phlebotomus* and of the diseases transmitted by these insects. Those authors also point out that as the life-cycle of *Phlebotomus* is long, a sandfly population takes a long time to build itself up again after being greatly reduced by D.D.T. It is likely that the use of D.D.T., gammexane and other modern insecticides will for most purposes largely supersede other methods of *Phlebotomus* control.

Personal protection. Sleeping on roofs or in upper storeys of houses does not always afford immunity from sandfly bites. The use of dimethyl phthalate as a repellent will give protection for several hours. The use of mosquito boots, smearing the exposed parts of the body with dimethyl phthalate in the evenings and sleeping under a sandfly net at night should give almost complete personal protection under any circumstances, e.g., during a temporary visit to a heavily infested place in which no other protective measures are taken.

II. STRUCTURE, SYNONYMY AND CLASSIFICATION.

ANATOMY.

The diagnostic characters of the subfamily PHLEBOTOMINAE are given on page 409, and detailed accounts of the anatomy of *Phlebotomus* will be found in the works of Grassi (1807), Newstead (1911), Perfiliew (1928). Separate studies have been published dealing with the structure of certain organs, e.g., pharynx, buccal cavity and spermatheca (Adler and Theodor, 1926), female genitalia (Sinton, 1927), the proboscis (Jobling, 1928), internal genital apparatus of the male (Parrot, 1937), ascoids, or "geniculated spines" (Parrot, 1940), and the ratio AIII/E (Parrot, 1946). Dolmatova (1942) discovered the existence of a peritrophic membrane in *P. papatasi*. The membrane can be seen in Sudan specimens of *P. papatasi*.

It will be unnecessary to give here more than an explanatory description of the characters which are important in the classification and identification of the Ethiopian species. For this purpose only the characters of the adults,

male and female, are important, since systematic work on the immature stages of *Phlebotomus* has been negligible so far. Many of the older works on *Phlebotomus* laid great emphasis on the measurements of various structures and the ratios between these measurements ("phlebotometry"). Much of this work has now been discarded, and only those measurements and ratios which have retained a useful place in systematics are considered here.

The position of hairs or spines on a segment or other structure can be conveniently indicated by the use of decimal numbers, a notation frequently used in this work. In all cases the proximal end of the segment or structure is taken as zero and the distal end as unity. Thus the statement that a segment bears a spine at 0.6 means that the spine arises at a point six-tenths of the length of the segment from its proximal end.

Practically all the examination of *Phlebotomus* is done with the microscope. Some of the characters used in specific determination are not always easy to make out. Hence it is extremely important to obtain good, clear preparations, otherwise details of structure are obscured and identification may be impossible. The methods of preparing and mounting specimens of *Phlebotomus* for examination are given on pages 500-501.

Head.

The antennae consist of 16 segments, usually indicated by roman numerals, I being the most proximal and XVI the most distal. Normally they are hairy, but the hairs are largely removed by the processes of clearing, etc., used in preparing mounted specimens. The first segment (scape) is small, the second (pedicel) is globular and cup-shaped, while segments III-XV are cylindrical, the terminal segment (XVI) having the form of a blunt cone. The measurements of segments III, IV and V and the length of III as compared with the combined lengths of IV and V are important in systematic descriptions in which III is shown as greater ($>$), less ($<$) than or equal to ($=$) $IV + V$. The ratio of the length of segment III to that of the epipharynx (AIII/E) is also important.

Newstead used the term geniculated spines for the spines borne on the antennal segments III-XV of *Phlebotomus*, and this term is used in most systematic descriptions. Tonnoir (1935) and Theodor (1947) conclude that these structures should be called ascoids, on the grounds that they are comparable with structures of this name found on the antennae of other PSYCHODIDAE and regarded by Feuerborn (1922) as sense organs. In *Phlebotomus* these spines are often difficult to see, and it may require the use of the oil-immersion lens to make out their structure clearly. Their number and disposition on the antennal segments are important; also the ratio of their length to that of the segment bearing them, segment IV being taken as typical, and whether their tips extend beyond or fall short of the line of articulation with the next segment.

The antennal formula is a convenient method of expressing in abbreviated form the number and disposition of the geniculated spines, or ascoids, on the antennal segments. In this formula the numerator, in arabic numbers, shows the number of the spines (1 or 2) present on each of the segments, and the denominator in roman numbers shows the serial numbers of the corresponding segments. Thus the antennal formula of a species with two ascoids on all the

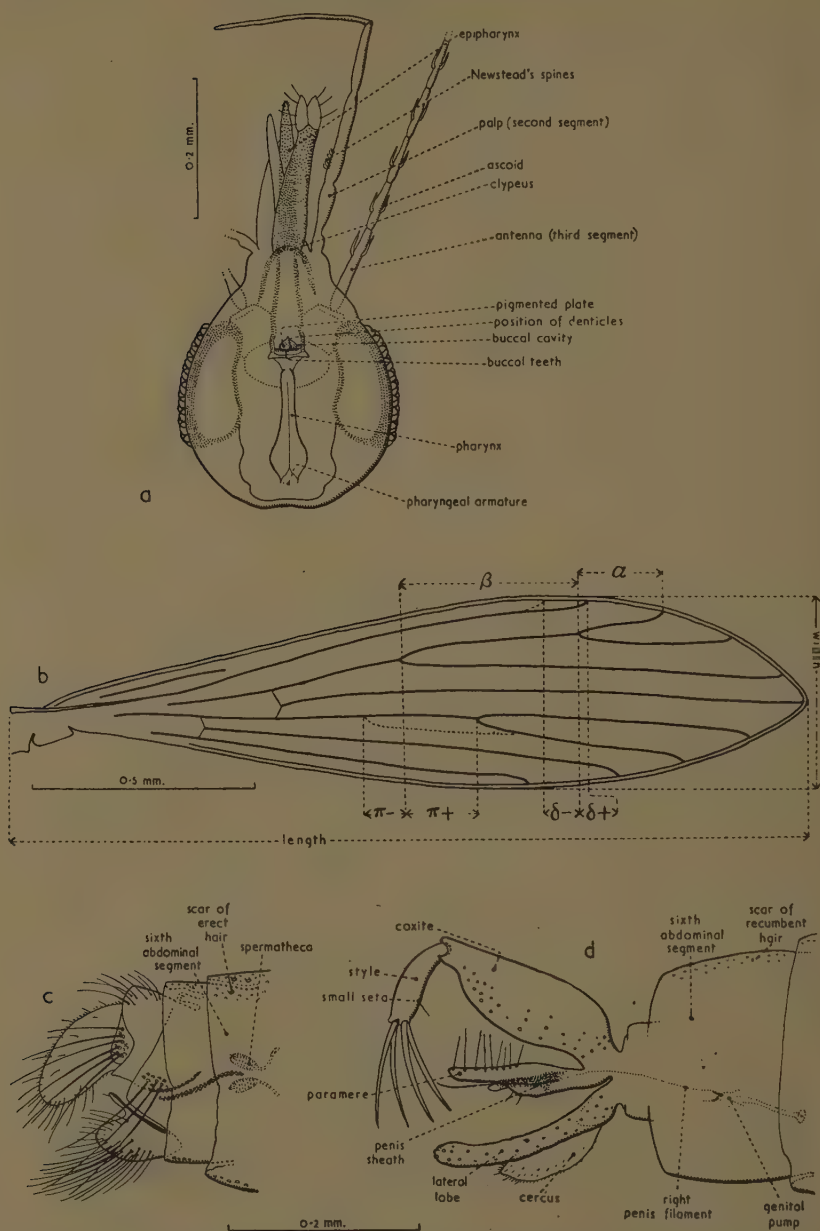


FIG. 1.—Showing the principal structures used in classification: *a*, head (*P. clydei*, ♀); *b*, wing (*P. bedfordi*, ♀); *c*, tip of abdomen of ♀ (*P. clydei*); *d*, terminalia of ♂ (*P. antennatus* var. *signatipennis*).

segments from III to XV inclusive would be 2/III-XV. The formulae of a specimen with two ascoids on segments III, IV, V, VI, VII and one ascoid only on the following segments (VIII-XV) would be 2/III-VII, 1/VIII-XV. The formula of a species which had two ascoids sometimes on III-VII and sometimes on III-VIII and a single spine on VIII-XV or IX-XV would be written 2, III-VII (VIII), 1/VIII (IX)-XV. As a rule the antennal formula shows sexual dimorphism in the subgenera *Sergentomyia* and *Sintonius*, that of the males being 1, III-XV and of the females 2, III-XV. Notable exceptions are *P. squamipleuris* 1/IV-XV in both sexes; *P. mirabilis* ♂ 2/III-VII; and *P. similimus* ♂, 1/IV, 2/V-XV. In the subgenus *Phlebotomus* there is no sexual dimorphism in the *papatasi* and *sergenti* groups (*Phlebotomus* and *Paraphlebotomus* of Theodor), the formula being 2/III-XV in both sexes. In the *majorchinensis* group (*Larroussius* and *Adlerius* of Theodor) the formula is usually 2/III-XV in the females and 2, III-VII (VIII), 1/VIII (IX)-XV in the males. Some unusual males are *P. rodhaini*, 2/III-XIII, 1/XIV-XV; *P. martini*, 2/III-X, 1/XI-XV; *P. katangensis*, 2/III-IX, 1/X. . .

Palps. The palps are composed of five segments generally designated by arabic numbers, 1 being the most proximal and 5 the most distal. In the palpal formula the numbers of the segments are written in order of increasing length of the segments. Thus a palpal formula of 1,2,4,3,5 indicates that 1 is shorter than 2, which is shorter than 4, which is shorter than 3, which in turn is shorter than 5. It is usual also to give the relative lengths of the palpal segments taking that of segment 1 as unity. For this purpose the figures expressing the relative lengths of the segments are arranged in the true anatomical order of the segments and not according to size. Specimens of *P. rodhaini* from the Sudan had a palpal formula of 1,4,2,3,5, the relative lengths of the segments being 1, 2.4, 3.6, 2.0, 4.6. When two segments are of equal size they are enclosed within brackets in the palpal formula. Thus in Newstead's type specimen of *P. bedfordi* the palpal formula is 1,2,3,(4,5), the relative lengths of the segments being 1, 3.75, 4.75, 6.25, 6.25. The structures known as Newstead's sensory spines occur on the second and third palpal segments in *P. squamipleuris*, but on the third segment only in other species.

The length of the epipharynx measured from the tip of the clypeus is an important measurement, and its relation to that of the third antennal segment; this is expressed by the ratio AIII/E, which may be greater or less than unity and is sometimes useful in differentiating closely similar species. The epipharynx is really a labrum-epipharynx, and is armed at its distal end with a fringe of specialized sensory hairs and spines which probably act as a sieve and prevent large particles from blocking the food channel.

The food channel is formed by the labrum-epipharynx and hypopharynx and is continued backwards into the prepharynx, a relatively long tube consisting of one dorsal and one ventral plate, the former with powerful retractor muscles. The semi-circular flange on its posterior wall which gives origin to the muscles attached to the salivary pump is its posterior limit. At this point it widens to form the mid-pharynx, or buccal cavity of systematic writers. Here also occur the characteristic lateral buccal protuberances in some species. The buccal cavity is a short, wide tube shaped like a truncated cone. About the middle of its widest part there are in some species a pigmented area of chitin on the dorsal wall and a series of teeth on the ventral wall—the so-called

buccal armature. In other species (subgenus *Phlebotomus* s. restr.) these structures are absent or rudimentary. In the species in which they occur the morphology of these structures is of the greatest importance in specific determination—the size and shape of the pigmented area, the number, size, shape and arrangement of the buccal teeth. In addition to the main row of buccal teeth there may be one or more rows of small anterior punctiform teeth, the arrangement of which is characteristic in different species. The use of the oil immersion lens may be necessary to show up clearly the details of the buccal armature.

The buccal cavity is continued posteriorly into the post-pharynx, or pharynx of systematic writers. This structure is composed of three chitinous plates, and is usually narrow anteriorly and wide posteriorly. Important measurements are its length, and the ratio between the widths of its anterior and posterior parts. Its shape is also characteristic in some species (e.g., cordiform, lamp-glass shaped, etc.). In most species the posterior part of the pharynx bears an armature of large or small spines, scales or ridges, and the character of this armature is of great importance in specific determination.

Thorax.

The wing of *Phlebotomus* is densely covered with hairs, but these very readily come off in the processes of clearing and mounting. Fig. 2*a, b* shows the wing of *Phlebotomus* with the venation numbered according to the older nomenclature and lettered according to the Revised Comstock Needham nomenclature as interpreted by Tonnoir (1935), who considers that Cu is a convex vein which is very short and that M has four well-developed branches. M₄ was previously interpreted as Cu by most authors. Equivalent terms in the two systems of nomenclature are given below :

<i>Old terminology</i>	<i>R.C.N. terminology.</i>
Auxiliary	
Subcosta	. Subcosta.
Mediastinal	
First longitudinal vein (R ₁)	. Radius, which divides into a simple
Second longitudinal vein (R ₂₊₃₊₄)	anterior branch, R ₁ and a primary
Third longitudinal vein (R ₅)	branch, the radial sector Rs, which
	divides into four branches.
Fourth longitudinal vein (M ₁₊₂)	. Media, with four branches.
Fifth longitudinal vein (M ₃)	
Sixth longitudinal vein (M ₄)	
	Cubitus.

It will be seen that in *Phlebotomus* the second longitudinal vein (Rs) is forked twice (to give R₂, R₃ and R₄) and the fourth longitudinal vein is forked once (to produce M₁ and M₂), giving the appearance of one long unforked vein, the third or R₅ lying between the two forked veins.

The length and breadth of the wing at its widest part are given in systematic descriptions. Theodor considers wing length is the best measurement to express quantitatively the relative sizes of different specimens. In the deter-

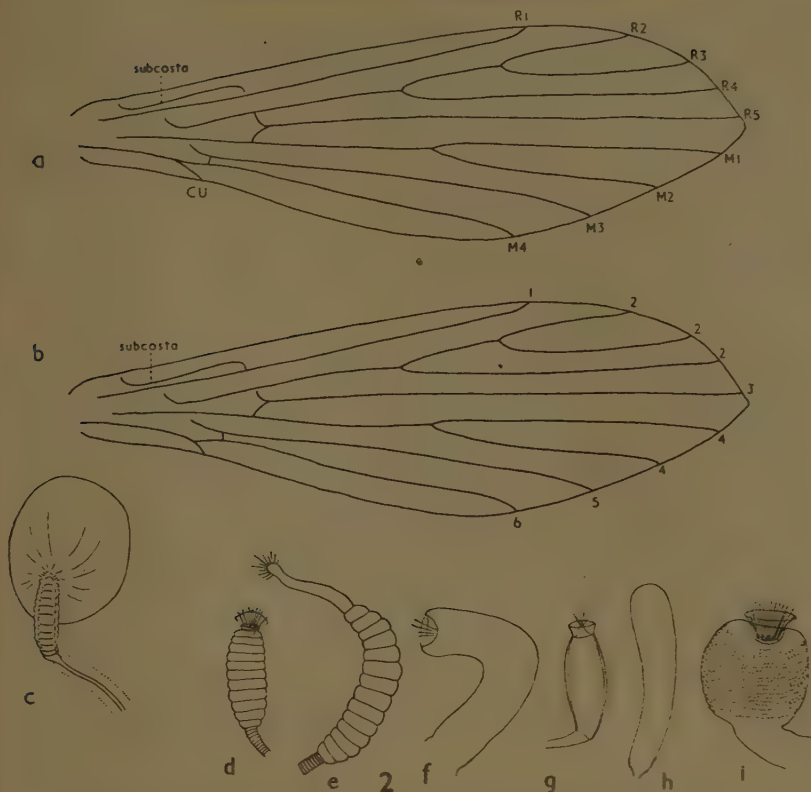


FIG. 2.—*a*, wing of *Phlebotomus* showing venation according to the RCN terminology (abbreviations explained in text); *b*, wing showing old nomenclature; *c*, fresh spermatheca of *P. papatasi* showing the position of the highly chitinized part. Principal types of spermatheca: *d*, segmented (*P. papatasi*); *e*, segmented, with neck (*P. longipes*); *f*, tubular (*P. schwetzi*); *g*, capsular (*P. freetownensis*); *h*, sac-like (*P. lesleyae*); *i*, globular (*P. squamipleuris*). (*c* after Newstead, 1911; *e* after Parrot and Martin, 1939; *f* after Adler, Theodor and Parrot, 1929; *g* after Theodor, 1948; *i* after Parrot, 1930).

mination of species certain measurements of the wing venation are useful. These are:

(1) The ratio of the anterior branch (α) to the stem (β) of the second fork of the second longitudinal vein. This ratio constitutes the alar index (α/β).

(2) The distance (δ) measured along the anterior border, between the extremity of the first longitudinal vein (R_1) and the projection on the anterior border of the second fork of the second vein (R_{2+3}) is prefixed by a + sign if the first vein overlaps the second radial fork as in the illustration (fig. 1 *b*) and by a - sign if it falls short of the second fork.

(3) The relative positions of the fork of the fourth vein and the first fork

of the second vein. The measurement between these two is designated by the symbol π , which is prefixed by a + sign if the first fork of the second vein lies nearer the base of the wing than the fork of the fourth vein, and by a — sign if the latter lies nearer the base of the wing.

The length of the hind leg is often included in systematic descriptions as a more accurate measurement of size than body length. In a few species spines are borne on the femora of the legs, and this is an important character in the species in which it is found, e.g., *P. affinis*, *P. wansonii*, *P. squamipleuris* var. *dreyfussi* and *P. christophersi* var. *calcaratus*. In *P. squamipleuris* the thoracic pleurae bear broad scales like those of mosquitoes, and those are not found in other species in the Old World.

Abdomen.

A very important character in the taxonomy of *Phlebotomus* is the disposition of the hairs on the tergites of abdominal segments II–VI. These hairs may be erect or recumbent, although in all species there are erect hairs of no taxonomic value on the thorax and dorsum of the first abdominal segment. In the processes of clearing and mounting the hairs are usually detached, but Sinton (1932) has pointed out that in mounted specimens, especially if stained, it is comparatively easy to determine the original disposition of the hairs from a study of the scars left on the abdominal tergites. The scars left by erect hairs are much larger and more refractile than those left by recumbent hairs. In species of the subgenus *Phlebotomus* the erect hairs on tergites II–VI are numerous, usually arranged in tufts at the distal ends of the segments. In the subgenus *Sergentomyia* the dorsal abdominal hairs on tergites II–VI are all recumbent (except in some specimens of *P. squamipleuris* which may have scanty erect hairs) and in the subgenus *Sintonius* there are numerous recumbent hairs with scanty erect hairs, the latter often confined to segments II and III, especially in the males.

In the females the highly chitinized parts of the spermathecae are important characters in the determination of species. In well-cleared specimens these structures can usually be made out inside the abdomen without dissection. The use of the oil-immersion lens is often a great help. The spermathecae vary considerably in structure and may be lightly or heavily chitinized, segmented or smooth, tubular, sac-like or capsular. In segmented or crenulated spermathecae the terminal tuft of hairs may be borne on a long or short "neck." In general the spermathecae are smooth in outline, or show only rudimentary and incomplete segmentation in the subgenus *Prophlebotomus*. They are segmented, or crenulated, in the subgenus *Sintonius*, although in a few species (but no Ethiopian ones so far) the segmentation may be incomplete. They are typically segmented in the subgenus *Phlebotomus*, but a few Ethiopian species of this subgenus have recently been described in which the spermathecae are smooth in outline, e.g., *P. lesleyae*, *P. heischii*. The character of the spermathecal ducts is sometimes important in systematics, whether they are narrow or wide, striated or smooth, and whether they open separately into the vulva or unite to form a common duct.

The chitinized parts of the internal genital apparatus of the male are often very conspicuous though of little systematic value. The pompetta or genital pump is a very efficient pumping apparatus constructed on the same plan as a

hypodermic syringe. The part corresponding to the plunger of the syringe is actuated by a series of small longitudinal muscles which arise from the button-like anterior dilatation and are inserted into the sides of the part corresponding to the barrel of the syringe. The distal opening of the syringe leads into the penis, and divides into two filamentous tubes which may be seen projecting from the distal end of that organ.

Terminalia.

The terminalia of the female are of little value in systematics (Sinton, 1927*d*), except in the case of *P. transvaalensis*, where the long and narrow cerci (fig. 29) and the eighth abdominal sternite bearing a number of stout very long bristles on its posterior border serve to distinguish this species from all other known species in the Ethiopian Region.

The terminalia of the male on the other hand vary considerably, and are of great importance in classification and specific determination. The terminology used by most authors in the description of the male terminalia of *Phlebotomus* is that developed by Newstead. Christophers and Barraud (1926) published a study of the development of the hypopygium of *Phlebotomus* in which the homology of the various parts was clarified. Tonnoir (1935) pointed out that retention of the older terminology is inconsistent with the rules now generally accepted in entomological literature, and that it should be altered to that indicated by the work of Christophers and Barraud, a suggestion endorsed by Theodor (1948). Equivalent terms in the two systems of nomenclature are given below:

<i>Newstead.</i>		<i>Christophers and Barraud.</i>
Proximal segment of superior clasper	=	Coxite.
Distal segment of superior clasper	=	Style.
Intermediate appendage	=	Parameres.
Intromittent organ	=	Penis (penis filaments + penis sheath).
Inferior claspers	=	Lateral lobes.
Submedian lamellae	=	Cerci.

Equivalent terms for the female terminalia have been omitted as they are not of systematic importance, but it is proposed in this work to employ throughout the terminology of Christophers and Barraud in descriptions of the male terminalia, which are of the greatest systematic importance. Relative measurements of the coxite, style parameres, penis and lateral lobe of the ninth tergite should be noted. The number, arrangement and shape of the spines or hairs borne on the style are very important. In some species the coxite also bears tufts of hair, either sessile or set on a peduncle, as in *P. sergenti* and its allies. The shape of the penis (sharp, blunt, conical, curved, etc.) may be an extremely useful character in differentiation, as is also that of the parameres (simple, double, or trilobed, and the characters of the various lobes).

SYNONYMY.

The synonymy of each species is given separately in a later section with the systematic descriptions. The present section deals with points of synonymy

in generic and subgeneric names, and some points in the synonymy of *P. minutus* and *P. africanus* which are important from the point of view of the nomenclature used in this work and which in some cases are not yet definitely settled.

The genus *Phlebotomus* was created by Rondani in 1840, and in 1843 he re-defined it and included in it three species, *P. papatasi* Scopoli, *P. molestus* Costa and *P. minutus* sp. n. Rondani in 1840 used the spelling "*Flebotomus*," in 1843 "*Hebotomus*" and in 1856 "*PHLOEBOTOMIDAE*." Costa Lima (1932) and Rapp (1942) have argued that the correct spelling of the generic name is that originally used by Rondani—"*Flebotomus*." Article 19 of the Rules of Nomenclature states that "the original orthography of a name is to be preserved unless an error of transcription, a *lapsus calami* or a typographical error is evident." Since the spelling *Phlebotomus* has been generally adopted the consensus of opinion appears to be to regard Rondani's original spelling, "*Flebotomus*," as due to a *lapsus calami* or a typographical error. In any case the name *Phlebotomus papatasi* has been included in a list of *nomina conservanda* as quoted by Handlirsch (1925). The spelling *Phlebotomus* will therefore be employed in this work.

Franca (1919) divided the genus *Phlebotomus* into two subgenera, *Phlebotomus* and *Newsteadia*, on the characters of the male terminalia. Franca and Parrot (1920), finding the name *Newsteadia* was preoccupied, changed the name of this subgenus to *Sergentomyia*, and suggested the creation of a third subgenus, *Neophlebotomus*, with *P. malabaricus* as the type species. No type species was defined for *Sergentomyia*, but in a later paper in the same year Franca (1920) named *P. minutus* Rondani as the type species for *Sergentomyia*. In 1921 Franca and Parrot proposed a more detailed system of classification in which *Sergentomyia*, Franca and Parrot, 1920, is subdivided into *Sergentomyia* (*pro parte*), in which the alar index is greater than unity, and *Prophlebotomus* in which the alar index is equal to or less than unity, and *P. minutus* is included in the new subgenus *Prophlebotomus*. Theodor (1948) points out that this is inadmissible under Article 29 of the Rules of Nomenclature, which states that "if a genus (or subgenus) is divided the type species has to remain with the restricted genus with the same name." He concludes therefore that *Prophlebotomus* has to be considered as a synonym of *Sergentomyia*. *Neophlebotomus* does not appear in the classification of Franca and Parrot (1921) but, as Theodor points out, according to more recent knowledge its type species (*P. malabaricus*) belongs to the same group as *P. minutus* and hence comes into the subgenus *Sergentomyia*, so *Neophlebotomus* also becomes a synonym of *Sergentomyia* and cannot be used again as was done by Dyar (1929), who used the name for certain New World species of *Phlebotomus*. It would appear from Theodor's analysis that the subsequent use of the name *Prophlebotomus* by Parrot (1934b) and by the present writers (1946) is inadmissible and that the correct name in this case is *Sergentomyia*. In this work, therefore, the name *Sergentomyia* will be used throughout in place of *Prophlebotomus*.

Difficulties have arisen in connection with the synonymy of *P. minutus* Rondani and *P. africanus* Newstead, which appear in the records as two of the commonest and most widely distributed species of *Phlebotomus* in Africa. It now appears that *P. minutus* is not an Ethiopian species but its synonymy has to be considered in an account of African sandflies.

The species *P. minutus* was created by Rondani in 1843, and later described by Newstead (1911) in an account of the sandflies of the Maltese Islands. In the following year Newstead (1912) separated *P. minutus* var. *africanus* from the typical *P. minutus* Rondani on account of its darker colour and certain differences in external characters. Fourteen years later Adler and Theodor (1926) drew attention to the internal characters (buccal cavity, pharynx and spermatheca) on which the determination of species of *Phlebotomus* is now largely based. In two Palestinian forms which had previously been determined on external characters as *P. minutus* and *P. minutus* var. *africanus*, they found that the differences in external characters were correlated with differences in internal structure and accordingly raised the variety to specific rank as *P. africanus* Newstead. A collection of *Phlebotomus* determined on external characters as *P. minutus* and *P. africanus* was found to contain *P. africanus* and two other species, one similar to the *P. minutus* of Palestine, the other a species which could not be differentiated from *P. minutus* on external characters, but showed very clear differences from *P. minutus* in the buccal cavity and pharynx. It was therefore described as *P. parroti* Adler and Theodor, 1927.

The discovery of the taxonomic importance of the buccal cavity, pharynx and spermatheca stimulated studies in *Phlebotomus*. In the following years many new species were described. *P. minutus* and *P. africanus* were recorded from many localities, and numerous varieties of both species were created, all based on the descriptions of Adler and Theodor. The specimens which Adler and Theodor had described under the names *P. minutus* and *P. africanus* were Palestinian ones, however, and not those for which the names had been originally introduced by Rondani and Newstead.

Sinton (1928a) examined one of Newstead's "cotype" (paratype) specimens of *P. minutus* from Malta and found that it agreed with the Palestinian form. Later, however, he states (Sinton, 1933) that "the species now commonly known as *P. minutus* Rondani is that described by Adler and Theodor (1926, 1927) from Palestine. It is doubtful whether this is the same as *P. minutus* Rondani from Italy. The latter may be synonymous with *P. parroti* Adler and Theodor, 1927." Parrot (1942, 1943a) found that the only *Prophlebotomus* occurring in Malta and Italy was in fact a variety of *P. parroti* (*P. parroti* var. *italicus* Adler and Theodor, 1931). He therefore concluded that this must be the original *P. minutus* Rondani and re-described it under this name in 1943. With the revelation that *P. minutus* Rondani was different from what it was generally believed to be, the Palestinian form originally described as *P. minutus* by Adler and Theodor was re-named *P. theodori*, and other forms which had previously been regarded as varieties of *P. minutus* were raised to specific rank as the simplest solution of the difficulty thus created.

Many of these forms are very similar to each other, being separated by minor differences only. Re-examination of Newstead's type specimens of *P. antennatus* by Kirk and Lewis (1950) shows that they are all closely allied to this species and might very well be regarded as varieties of it. In this work the Ethiopian forms previously regarded as varieties of *P. minutus*, and some allied species, are treated as varieties of *P. antennatus* Newstead. *P. minutus* Rondani is essentially a Palaearctic species and does not occur in the Ethiopian Region. Previous records of this species are therefore invalid as they refer to some other species, most commonly *P. antennatus* or one of its varieties.

The position is somewhat similar in the case of *P. africanus*, about which there are several discrepancies in the literature referring to the type. Adler, Theodor and Parrot (1929) depict *P. africanus* from the Belgian Congo with no anterior small teeth in the buccal cavity. Theodor (1933) states that the form which occurs in the Sudan and Congo is typical, and depicts the buccal armature of this form as having anterior punctiform teeth. Sinton (1928a) examined one of Newstead's paratypes from Southern Nigeria, and concluded it was identical with the Palestinian form described by Adler and Theodor. Newstead's original specimens came, however, from North-Eastern Rhodesia. The numerous varieties of *P. africanus* now recorded from Africa and elsewhere were created without reference to this specimen and on taxonomic characters which were not recognized by Newstead. Re-examination of Newstead's type-specimens by the present writers has shown that they are quite different from the *P. africanus* of Adler and Theodor (1926) and all subsequent authors. Also there are some important discrepancies between Newstead's written description and the labels on the specimens.

The type series, including a specimen clearly labelled "type ♀" in Newstead's writing, is mainly *P. squamipleuris* or a variety of this species, but includes other species. It is difficult to believe that in designating type-specimens of *P. minutus africanus* Newstead could have missed such an unusual species as *P. squamipleuris* Newstead, especially as the two species were described in the same paper. Also to accept this conclusion would require exchanging the names of two common species. To avoid this a petition is being submitted to the International Commission on Zoological Nomenclature asking for the suppression of the name *africanus* for ever. This will enable the name *squamipleuris* to be retained for the species at present known by that name, and a new name has to be found for the species and varieties now known under the name *africanus*. Following orthodox practice we suggest the adoption of the name of the first synonym or subspecies of *africanus*, viz., *P. fretownensis* Sinton, 1930.

P. fretownensis was described by Sinton (1930) from one female specimen collected by Sir Rickard Christophers at Sierra Leone in September, 1926. The specimen was at first thought to be a variety of *P. africanus*, but so many points of difference were found between it and the Palestinian form of *P. africanus* (subsequently known as var. *asiaticus*) that it was given specific rank as *P. fretownensis*. Theodor (1948) later concluded it should be regarded as merely a variety of *P. africanus*. We have been unable to trace the specimen, but Sinton's detailed descriptions and figures define it with precision. It differs in some minor details from the typical African form of *P. africanus* Newstead described by Adler, Theodor and Parrot (1929) from the Belgian Congo. As pointed out by Theodor (1948), the latter appears to be identical with the form described by Sinton (1932) as *P. africanus* var. *magnus*, which now becomes *P. fretownensis* var. *magnus*. The only alteration in nomenclature required as regards the other varieties of *P. africanus* is that they become instead varieties of *P. fretownensis*.

CLASSIFICATION.

The sandflies (PHLEBOTOMINAE) belong to the PSYCHODIDAE, a family of the lower or simple Diptera. Alexander (1929) subdivided the PSYCHODIDAE

into four sub-families, PSYCHODINAE, TRICHOMYIINAE, BRUCHOMYIINAE and PHLEBOTOMINAE on the characters of the wing venation, and this classification has been accepted by Tonnoir, Edwards and Theodor. Only the PHLEBOTOMINAE are blood-suckers, by which character and the wing venation they are readily separated from all other PSYCHODIDAE. The characters of the sub-family PHLEBOTOMINAE may be summarized as follows :

Eyes round. Palps with five, antennae with 16 segments. Mouthparts adapted for piercing and blood-sucking. Wings held away from body at an angle of 45 degrees. Rs four-branched, pectinated, R_4 originating in middle of wing, R_5 originating proximal to R_4 from Rs near wing base. Cu very short, A absent. According to the old nomenclature the second longitudinal vein is forked twice and the fourth longitudinal vein forks once, giving the appearance of one long unforked vein, the third, between the two forked veins.

Attempts to classify the species of the PHLEBOTOMINAE have been made from time to time. Most of them follow the same general lines but differ considerably in the details. Most authors classify the PHLEBOTOMINAE in a single genus *Phlebotomus*, but Theodor has proposed a division into four genera, with several subgenera. Since the different classifications suggested often entail differences in nomenclature and no system has yet been universally accepted, the various schemes which have been proposed for the Old World species are summarized and briefly discussed below. According to Theodor (1948) the New World species are not well enough known for a definite classification. Most of the species which have been fully described have a buccal armature which differs from that of the Old World species, but a few of the species have no armature. It is uncertain at present whether the American species without a buccal armature can be put into the same group as the Old World species without a buccal armature or will have to be separated. Theodor puts them provisionally into a separate genus, *Brumptomyia* Franca and Parrot, the American species with a buccal cavity being placed in the genus *Lutzomyia* Franca.

Early Classifications.

Newstead (1911) divided the sandflies of the Maltese Islands into two groups : (i) those in which the hairs on the dorsum of the abdomen are erect, and (ii) those in which these hairs are recumbent. A similar division was used by Sinton (1924) in compiling a diagnostic table of the males of the Indian species.

Franca (1919) made an attempt to classify the species of *Phlebotomus* by dividing them into two subgenera on the characters of the male genitalia. After suggesting various modifications of this system, which are mentioned on page 406, Franca and Parrot (1921) divided the genus into five subgenera, namely, *Phlebotomus*, *Prophlebotomus*, *Brumptomyia*, *Lutzia* (emend *Lutzomyia* Franca, 1924) and *Sergentomyia*. In this classification *Prophlebotomus* was separated from the other subgenera by the alar index being less than unity in *Prophlebotomus*, and greater than or equal to unity in the other subgenera. The remaining subgenera were separated according to differences in the male genitalia. This classification was unsatisfactory in many ways. In a later publication Parrot (1934) points out that the scheme was conceived as a guide to further work and research rather than as a categorical affirmation of definitive characters.

Classification of Sinton.

In 1926 Adler and Theodor showed from an examination of Palestine sandflies that in certain species the posterior portion of the buccal cavity bears a number of teeth and a pigmented area of chitin, which are absent in other species. They showed further, that the morphology of these structures and of the pharynx and spermatheca were of diagnostic value in the determination of species. In 1927 Sinton found that Newstead's division into erect- and recumbent-haired species was correlated with definite morphological characters in the buccal cavity and spermatheca, species of the erect-haired group having no buccal armature and spermathecae with a crenulated or segmented appearance, while in those of the recumbent-haired group the spermatheca has a smooth outline and a buccal armature is present. Sinton (1927a) proposed a division of the genus into three main divisions, which were further subdivided, as follows.

A. The Erect-haired Division.

The members of this division have always some erect hairs on the dorsal aspects of segments II to VI of the abdomen. The heavily chitinized parts of the spermathecae of the females of this division are segmented in their entire length. The species in this division may be arranged into two groups:

Group 1: The erect abdominal hairs are numerous, usually occurring in tufts at the distal ends of the segments; dorsal recumbent hairs very scanty or absent on abdominal segments II to VI; buccal armature and pigmented area absent or rudimentary; the spermathecal chitinizations and male hypopygium usually having specific characters and the pharyngeal armature showing a useful diagnostic morphology.

Group 2: Species with scanty erect hairs on the dorsal aspects of abdominal segments II to VI; such hairs often confined to segments II and III, especially in the males; dorsal recumbent hairs usually numerous; buccal armature and pigmented area usually well developed and with specific morphology.

B. The recumbent-haired Division.

In this division the dorsal abdominal hairs on segments II to VI are all recumbent: the body of the spermathecal chitinizations usually with smooth outline, and any traces of segmentation, if present, are confined to the distal end. The buccal armature and pigmented area are usually well developed and have a specific morphology. The division contains two groups:

Group 3: In these the morphology of the male genitalia closely resembles that of *P. minutus* Rondani.

Group 4: The morphology of the male genitalia is distinctly different from that of *P. minutus* Rondani.

C. The intermediate Division.

Only one species, *P. squamipleuris*, is contained in this division. This species may show a few erect hairs on the dorsal aspects of some of the abdominal segments from II to VI, but more usually all the hairs are recumbent in this position. The spermathecal chitinizations are not crenulated, but show a series of transverse rows of small spines. This species differs from all others

in that the thoracic pleurae carry tufts of broad scales like those seen in mosquitoes, in the unilateral geniculate spines of the antennae of the female, in the absence of these spines on segment III, and in the presence of Newstead's sensory spines on both the second and third palpal segments.

Later Classifications.

Other workers who have attempted the classification of *Phlebotomus* (Nitzulescu, 1931; Theodor, 1931) appear to regard the buccal cavity as of greater value than the disposition of the hairs on the abdominal tergites, and divide the genus into two primary divisions—species which possess a buccal armature and those without a buccal armature. Nitzulescu found that, in spite of its apparent simplicity, Sinton's primary division into erect- and recumbent-haired species was not always easy to determine in practice (but see page 404) and proposed a division of the genus into five subgenera as follows:

A. Possessing a well-marked buccal armature.

1. Spermatheca segmented Subgenus *Sintonius*.
2. Spermatheca not segmented Subgenus *Brumptius*.

B. Buccal cavity without teeth and pigmented area.

3. Spermatheca segmented, with long neck . . . Subgenus *Larroussius*.
4. Spermatheca segmented with short neck . . Subgenus *Phlebotomus*.
5. Spermatheca smooth ("lisse") Subgenus *Adlerius*.

Parrot (1934b) takes exception to this classification on the grounds that it places closely related species like *P. major* and *P. chinensis* in different subgenera, whereas such diverse forms as *P. papatasi*, *P. argentipes* and *P. sergenti* are grouped together in one subgenus, and also because the classification depends entirely on the characters of the female and does not take into account the male genitalia, the importance of which was recognized by previous workers. Parrot agrees, however, with the primary division into species which possess a well-developed buccal armature and those which do not, but states his opinion that it is hardly justifiable in the present state of knowledge to undertake any further subdivision of the genus at the present time, at least as far as the Old World species are concerned. He points out that the first group corresponds in large measure with the subgenus *Prophlebotomus* of Franca and Parrot (1921), and divides the genus into two subgenera, which are defined as follows:

Phlebotomus: Bouche inerme; indice alar supérieur ou au moins égal à l'unité; poils des tergites abdominaux uniformément dressés; parasites habituels des animaux à sang chaud. Type: *P. papatasi* (Scop., 1896).

Prophlebotomus: Franca et Parrot, 1921: bouche armée de dents; indice alar généralement inférieur ou à peine égal à l'unité; poils des tergites abdominaux uniformément ou presque uniformément couchés; parasites habituels des animaux à sang froid. Type: *P. minutus* Rondani, 1843.

Sinton (1928a) found wing venation a variable character, unsuitable for primary division, as did Magnitsky and Gutzewitsch (1929), while several species of the subgenus *Prophlebotomus* have since been recorded as vicious biters of man (cf. Kirk and Lewis, 1940). The primary division into those forms which have a buccal armature and those which do not is, however, a

convenient one, because it enables any single male or female, the precise determination of which is doubtful, to be assigned to the appropriate group.

It will be seen that the subgenus *Phlebotomus* of Parrot's classification corresponds with Sinton's group I. Groups 2, 3, 4 and the intermediate division of Sinton are all included in the subgenus *Prophlebotomus*. The species in Sinton's group 2 form a fairly homogeneous group, presenting specific features, which, if the morphology of the spermatheca and hairs on the abdominal tergites be taken into consideration, are rather intermediate between *Phlebotomus* and the other members of the subgenus *Prophlebotomus* as defined by Parrot (1934b). The females correspond with Nitzulescu's definition of the subgenus *Sintonius*, and there is considerable uniformity among the males of this group, all those which have been described so far having terminalia of the *minutus* type with hooked parameres and pointed penis. Kirk and Lewis (1946) therefore, suggested a modification of Parrot's (1934b) classification in which the Ethiopian species were divided into three subgenera, *Phlebotomus* Rondani, 1840, *Prophlebotomus* Franca and Parrot, 1921, and *Sintonius* Nitzulescu 1931. *Sintonius* differs from *Phlebotomus* in having a buccal armature, and from *Prophlebotomus* in having scanty erect hairs on the abdominal tergites and segmented spermathecae and may be considered as intermediate between the other two subgenera. Of the three subgenera suggested by Kirk and Lewis *Sintonius* is the most homogeneous. The subgenus *Phlebotomus* includes several forms, such as *P. gigas*, *P. lesleyae* and *P. heischii*, in which the spermathecae are peculiar. In the subgenera *Phlebotomus* and *Prophlebotomus* (= *Sergentomyia*) of Kirk and Lewis there is considerable variety in the structure of the male, and this has been made the basis of further subdivision by Sinton (1927) and Theodor (1948).

Theodor (1948) has proposed a much more elaborate classification of the PHLEBOTOMINAE. He recognizes two genera in the old World, *Phlebotomus* s. restr. and *Sergentomyia*, corresponding with the subgenera *Phlebotomus* and *Prophlebotomus* of Parrot (1934). The genus *Phlebotomus* is divided into nine subgenera—*Phlebotomus* s. restr., *Paraphlebotomus*, *Synphlebotomus*, *Larrousius*, *Adlerius*, *Euphlebotomus*, *Anaphlebotomus*, *Australophlebotomus* and *Spelaeophlebotomus*—on the characters of the pharynx, spermatheca and male terminalia. *Sergentomyia* is divided into three subgenera—*Sergentomyia* s. restr. (sub-divided into a number of groups which are not given special names), *Sintonius* and *Spelaeomyia*. Apart from the creation of two genera and the introduction of many new names of subgenera, the classification of Theodor follows the same general lines as previous attempts.

It is doubtful at present whether Theodor's classification will become generally accepted or not. Parrot (1951) criticizes it severely in a recent paper. Hence in this work we propose to retain meantime the simpler classification of Kirk and Lewis (1946), in which all the PHLEBOTOMINAE are included in one genus, *Phlebotomus*. We classify the Ethiopian species of *Phlebotomus* into three subgenera, *Phlebotomus*, *Sintonius* and *Sergentomyia* (= *Prophlebotomus*), defined as follows:

Phlebotomus s. restr.

Species with numerous erect hairs on the abdominal tergites II to VI, usually occurring in tufts on the distal ends of the segments; buccal armature and pigmented area absent or rudimentary; the heavily chititized parts of the spermathecae usually segmented in

their entire length; spermathecal chitinizations and male hypopygium usually having specific characters.

Sintonius Nitzulescu, 1931.

Species with scanty erect hairs on the dorsal aspects of abdominal tergites II to VI, such hairs often confined to segments II and III, especially in the males; dorsal recumbent hairs usually numerous; buccal armature and pigmented area usually well developed and showing a specific morphology; spermathecae crenulated; male hypopygium usually of the *minutus* type, with pointed penis sheath and hooked or beaked paramere.

Sergentomyia Franca and Parrot, 1920, (= *Prophlebotomus* Franca and Parrot, 1921; Parrot, 1934; Kirk and Lewis, 1946.)

Species with dorsal hairs on abdominal segments II to VI all recumbent; buccal armature and pigmented area usually well developed and with specific morphology; the body of the spermathecal chitinizations usually with a smooth outline, and any traces of annulation, if present, confined to the distal end.

The easily recognizable characters of the subgenus *Sintonius* as defined above are confined to the females. In species which are known only by the male it may be difficult to differentiate between *Sintonius* and *Sergentomyia*, as terminalia of the *minutus* type occur in both subgenera. We have found, however, that there is one character by which the males of the subgenus can generally be differentiated (with the exception of *P. squamipleuris*, which is abnormal in other characters) from those of the subgenus *Sergentomyia* with terminalia of the *minutus* type. This character is the relatively large sixth abdominal segment, which is often evident on examination with a hand lens. In addition, Sinton (1932) has pointed out that in specimens which have been mounted, especially if stained, it is comparatively easy to determine the original disposition of the hairs on the abdominal tergites from a study of the scars left on the segments by these hairs.

VARIATION.

There are no agreed definitions of the terms "species" and "variety," and the limits of these categories are generally fixed according to the judgment of the taxonomist. Aberrant forms or ecological variants which are entirely phenotypic modifications may be described as new species by the systematist, but in modern systematics there is a tendency for the classical method in which categories are separated from one another by the degree of morphological differentiation to be supplemented by other methods of analysis which elucidate the role played by variation. Owing to lack of detailed information this has rarely been possible in the case of *Phlebotomus*, many species of which are known only from a short museum series, or even a single specimen. Parrot (1936b), however, resorted to breeding experiments for the differentiation of *P. perniciosus* and *P. longicuspis*, two closely allied species which were found always in close association with each other in various localities in Algeria.

Although little is known about variation in *Phlebotomus*, two aspects of the subject may be mentioned in connection with systematics.

Abnormalities. Like other animals specimens of *Phlebotomus* sometimes show obvious abnormalities. Variations in the size and shape of the pigmented area are not uncommon. We have encountered occasional specimens of *P. ingrami* and *P. bedfordi* var. *congolensis* in which the pigmented area was

completely absent, although this structure is normally conspicuous in both species. Parrot and Habibi (1947) have reported some striking abnormalities in wild caught specimens of *P. minutus* var. *parroti*. Newstead (1914), Newstead and Sinton (1921) and Parrot (1921) have reported supernumerary spines on the style of various species. It is extremely likely that the specimens described as *P. mascittii* by Grassi (1908) were aberrant forms of *P. larroussei* with a supernumerary spine on the style, so that *P. larroussei* becomes a synonym of *P. mascittii*. Theodor (1948) suggests that *P. hirtus*, a species known by one male only, may be an aberrant form of this nature, on account of the unusually large number of spines on the style.

Geographical races. Compared with many other insects *Phlebotomus* appears to have a marked tendency to the development of local races and varieties (Theodor, 1933), probably owing to its delicacy and limited powers of flight. Sutton (1950) considers that *P. papatasi* from Malta, Algiers, Italy, India and the Sudan can be differentiated from each other by minor characters. Theodor (1947) states that there are at least five different forms of *P. chinensis* from India, Persia, Syria, Cyprus and Roumania which may eventually have to be separated as varieties or species. Lewis and Kirk (1939) have described differences between the African and Indian forms of *P. clydei*. Differences between the African and Indian forms of *P. squamipleuris* have led to the separation of the latter as var. *indicus* (Theodor, 1931). *P. freetownensis* and its numerous varieties which have been collected in large numbers from many localities will probably, on further analysis, provide interesting data on variation in its geographical aspect.

Many of the species and varieties now separated from each other by minor differences only may be shown after further study to be geographical races. Two very closely allied forms, *P. antennatus* var. *cinctus* and *P. antennatus* var. *signatipennis*, are practically mutually exclusive in their distribution in the Sudan, var. *cinctus* being almost restricted to the southern and var. *signatipennis* to the northern half of the country. Kirk and Lewis (1947) noted that sandflies from the arid northern regions of the Sudan tend to be less heavily pigmented than those from the more humid south, and it is possible that the differences between *P. schwetzi* and its variety *nigricans* are due essentially to the expression of this tendency.

Discussing geographical races in *P. major*, Adler (1946) points out that in addition to minute morphological differences there are also some striking differences in bionomics among the Mediterranean races of this species. He suggests that these may, in the case of *P. major*, prove to be important in the epidemiology of visceral leishmaniasis, since in other groups of sandflies it has been found that slight differences in morphology may be accompanied by profound differences in bionomics and capacity to transmit disease.

III. KEYS TO THE ETHIOPIAN SPECIES.

List of the Ethiopian Species of Phlebotomus.

The following list comprises all the species and varieties of *Phlebotomus* at present recognized as occurring in the Ethiopian Region arranged in the order in which they are described in this work.

Subgenus *Phlebotomus*.

<i>P. (P.) papatasi</i>	p. 421	<i>P. (S.) cowlandi</i>	p. 462
<i>P. (P.) papatasi</i> var. <i>bergeroti</i>	p. 423	<i>P. (S.) richardi</i>	p. 463
<i>P. (P.) roubaudi</i>	p. 424	<i>P. (S.) schoutedeni</i>	p. 463
<i>P. (P.) roubaudi</i> var. <i>fourtoni</i>	p. 425	<i>P. (S.) schoutedeni</i> var. <i>pungens</i>	p. 464
<i>P. (P.) duboscqi</i>	p. 427	<i>P. (S.) yusafi</i>	p. 465
<i>P. (P.) alexandri</i>	p. 427	<i>P. (S.) pastorianus</i>	p. 466
<i>P. (P.) sergenti</i>	p. 428	<i>P. (S.) buxtoni</i>	p. 467
<i>P. (P.) sergenti</i> var. <i>saevus</i>	p. 429	<i>P. (S.) aretasi</i>	p. 468
<i>P. (P.) katangensis</i>	p. 430	<i>P. (S.) simillimus</i>	p. 469
<i>P. (P.) martini</i>	p. 431	<i>P. (S.) schwetzi</i>	p. 470
<i>P. (P.) rossi</i>	p. 431	<i>P. (S.) schwetzi</i> var. <i>nigricans</i>	p. 471
<i>P. (P.) orientalis</i>	p. 432	<i>P. (S.) guiraudi</i>	p. 471
<i>P. (P.) longipes</i>	p. 434	<i>P. (S.) freetownensis</i>	p. 472
<i>P. (P.) lesleyae</i>	p. 435	<i>P. (S.) freetownensis</i> var. <i>magnus</i>	p. 472
<i>P. (P.) heischii</i>	p. 436	<i>P. (S.) freetownensis</i> var. <i>ater</i>	p. 474
<i>P. (P.) rodhaini</i>	p. 437	<i>P. (S.) freetownensis</i> var. <i>eremitis</i>	p. 474
<i>P. (P.) gigas</i>	p. 438	<i>P. (S.) freetownensis</i> var. <i>longior</i>	p. 475

Subgenus *Sintonius*.

<i>P. (S.) adleri</i>	p. 439	<i>P. (S.) freetownensis</i> var. <i>meridianus</i>	p. 475
<i>P. (S.) affinis</i>	p. 440	<i>P. (S.) freetownensis</i> var. <i>niger</i>	p. 477
<i>P. (S.) affinis</i> var. <i>vorax</i>	p. 441	<i>P. (S.) freetownensis</i> var. <i>sudanicus</i>	p. 477
<i>P. (S.) caffericus</i>	p. 442	<i>P. (S.) babu</i>	p. 478
<i>P. (S.) christophersi</i>	p. 443	<i>P. (S.) crosarai</i>	p. 479
<i>P. (S.) christophersi</i> var. <i>calcaratus</i>	p. 444	<i>P. (S.) yvonnae</i>	p. 480
<i>P. (S.) clydei</i>	p. 445	<i>P. (S.) ingrami</i>	p. 480
<i>P. (S.) meilloni</i>	p. 446	<i>P. (S.) serratus</i>	p. 482
<i>P. (S.) meilloni</i> var. <i>suberectus</i>	p. 447	<i>P. (S.) kirki</i>	p. 483
<i>P. (S.) subtilis</i>	p. 447	<i>P. (S.) notatus</i>	p. 484
<i>P. (S.) thomsoni</i>	p. 449	<i>P. (S.) collarti</i>	p. 485
<i>P. (S.) transvaalensis</i>	p. 450	<i>P. (S.) decipiens</i>	p. 486
<i>P. (S.) wansonii</i>	p. 451	<i>P. (S.) durenti</i>	p. 487
		<i>P. (S.) squamipleuris</i>	p. 488
		<i>P. (S.) squamipleuris</i> var. <i>dreyfussi</i>	p. 489

Subgenus *Sergentomyia*.

<i>P. (S.) renauxi</i>	p. 452	<i>P. (S.) squamipleuris</i> var. <i>inermis</i>	p. 491
<i>P. (S.) antennatus</i>	p. 452	<i>P. (S.) wurtzi</i>	p. 491
<i>P. (S.) antennatus</i> var. <i>signatipennis</i>	p. 454	<i>P. (S.) horgani</i>	p. 492
<i>P. (S.) antennatus</i> var. <i>cinctus</i>	p. 456	<i>P. (S.) lewisi</i>	p. 493
<i>P. (S.) antennatus</i> var. <i>occidentalis</i>	p. 455	<i>P. (S.) hunti</i>	p. 494
<i>P. (S.) antennatus</i> var. <i>dubius</i>	p. 457	<i>P. (S.) rutledgei</i>	p. 495
<i>P. (S.) bedfordi</i>	p. 458	<i>P. (S.) lumsdeni</i>	p. 496
<i>P. (S.) bedfordi</i> var. <i>congolensis</i>	p. 459	<i>P. (S.) hirtus</i>	p. 497
<i>P. (S.) bedfordi</i> var. <i>firmatus</i>	p. 460	<i>P. (S.) mirabilis</i>	p. 497
<i>P. (S.) bedfordi</i> var. <i>medius</i>	p. 461	<i>P. (S.) wynnai</i>	p. 499

For convenience of reference we give below a list of synonyms, which also includes the names of species erroneously recorded from the Ethiopian Region.

<i>aethiopicus</i>	p. 470	<i>distinctus</i>	p. 458
<i>brodeni</i>	p. 469	<i>ghesquieri</i>	p. 488

<i>iraqi</i>	p. 488	<i>raptus</i>	p. 481
<i>langeroni</i>	p. 432	<i>sanneri</i>	p. 454
<i>matadiensis</i>	p. 451	<i>symesi</i>	p. 470
<i>mathisi</i>	p. 467	<i>tiberiadis</i>	p. 447
<i>minutus</i>	p. 407	<i>vagus</i>	p. 445
<i>molesta</i>	p. 422	<i>viator</i>	p. 445
<i>nairobiensis</i>	p. 459	<i>viduus</i>	p. 423
<i>perniciosus</i>	p. 432		

KEY TO THE SUBGENERA, FEMALES.

1. Buccal armature and pigmented area absent or very rudimentary *Phlebotomus*.
Buccal armature well-developed and with distinctive morphology 2.
2. Spermatheca crenulated *Sintonius*.
Spermatheca not crenulated *Sergentomyia*.

KEY TO THE SUBGENERA, MALES.

1. Buccal armature and pigmented area absent or very rudimentary;
abdominal tergites II-VI with numerous erect hairs *Phlebotomus*.
Buccal armature and pigmented area usually well-developed; abdominal tergites II-VI with scanty or no erect hairs 2.
2. Abdominal tergites II-VI with scanty erect hairs *Sintonius*.
Abdominal tergites II-VI with numerous recumbent and no erect hairs *Sergentomyia*.

Key for the Females of the Subgenus *Phlebotomus*.

1. Females with numerous erect hairs on dorsal aspect of abdominal segments II-VI, usually in tufts at the distal end of the segment.
Buccal armature and pigmented area absent or rudimentary 2.
2. Spermatheca sac-like, not segmented 3.
Spermatheca segmented in entire length 5.
3. Alar index = 5 or 6; a specialized, very large, cave-dwelling species
gigas (p. 438).
Alar index = 0.3 4.
4. Ascoids long (0.6 length of segment) *heischi* (p. 436).
Ascoids short (0.2 length of segment) *lesleyae* (p. 435).
5. Spermatheca with a long neck; pharyngeal armature consists of rows of very small point-like teeth 6.
Spermatheca not provided with long neck 7.
6. Spermatheca with 10-12 segments; the terminal (non-annulated) dilated part of spermathecal duct long (= $\frac{1}{3}$ of total length of duct)
orientalis (p. 432).
Spermatheca with 12-14 segments; terminal (non-annulated) dilatation of spermathecal duct short *longipes* (p. 434).
7. Pharyngeal armature composed of coarse teeth; spermatheca with only 4-6 segments, without expanded head *sergenti* and var. (p. 428)
alexandri (p. 427).
Spermatheca with more than 5 segments; pharyngeal teeth less marked 8.

8. Pharyngeal armature composed of fine ridges and small punctiform teeth; spermatheca has 9-10 segments *martini* (p. 431).
Pharyngeal armature appearing as a network of fine wavy lines; spermatheca with 8-12 segments, and large expanded head, with no neck *papatasi* and var. (p. 421).
roubaudi (p. 424).
duboscqi (p. 427).

Key for the Males of the Subgenus *Phlebotomus*.

- | | |
|---|------------------------------------|
| 1. Males with numerous erect hairs on abdominal tergites II-VI; buccal armature and pigmented area absent or rudimentary; genitalia usually having a specific morphology | 2. |
| 2. Coxite bearing on its inner aspect a prominent tuft of hairs arising from a peduncle | 3. |
| Coxite without such tuft of hairs | 7. |
| 3. Style bearing 4 spines | 4. |
| Style bearing 5 spines | 5. |
| 4. One of the distal spines on the style apical, the other subapical; peduncle bearing the tuft of hairs on coxite short | <i>alexandri</i> (p. 427). |
| The two distal spines on style both terminal (except in var. <i>saevus</i> , in which the peduncle bearing the tuft of hairs is elongated) | <i>sergenti</i> and var. (p. 428). |
| 5. Peduncle on coxite bearing long hairs of uniform length and shape | <i>katangensis</i> (p. 430). |
| Peduncle bearing hairs of different length and shape | 6. |
| 6. Peduncle on coxite bearing about 4 very long bristles apically and a large number of shorter hooked bristles ventrally, the latter decreasing in size from near the apex to the base | <i>rossi</i> (p. 431). |
| Peduncle bears a tuft of 6 large flat hairs and about 12 shorter slender hairs, with no regular gradation in size | <i>martini</i> (p. 431). |
| 7. Style bearing 4 spines | 8. |
| Style bearing 5 spines | 9. |
| 8. Paramere bilobed, with characteristic morphology | <i>rodhaini</i> (p. 437). |
| Paramere single, finger-shaped | <i>gigas</i> (p. 438). |
| 9. Style very elongate, having parallel sides, and bearing 5 short spines; lateral lobe bearing 2-6 apical spines; paramere with 3 characteristic lobes | 10. |
| Style irregular in shape, bearing 5 long spines | 11. |
| 10. Lateral lobe with 4-6 very short terminal spines | <i>roubaudi</i> (p. 424). |
| Lateral lobe with 2 long terminal spines | <i>papatasi</i> (p. 421). |
| 11. Paramere consisting of an upper lobe bearing hairs, a lower lobe composed of a stem bearing a few hairs, and a thin broad smooth plate | <i>lesleyae</i> (p. 435). |
| Paramere simple | 12. |
| 12. Paramere with expanded distal end cut away ventrally; single point of penis sheath directed dorsally | <i>longipes</i> (p. 434). |
| Paramere less expanded and more rounded at distal end; single point of penis sheath directed infero-externally | <i>orientalis</i> (p. 432). |

Key for the Females of the Subgenus *Sintonius*.

- | | |
|--|----|
| 1. Females having both erect and recumbent hairs on dorsal aspects of abdominal segments II-VI, well-developed buccal armature, and crenulated spermathecae, with short neck | 2. |
|--|----|

2. Cerci long and narrow; sternite of 8th abdominal segment with a number of stout, very long bristles arising from its posterior border
transvaalensis (p. 450). 3.
- These features not present 3.
3. Buccal armature with anterior teeth 4.
- Buccal armature consisting of a single row of teeth; no anterior punctiform teeth 7.
4. Several (three or more) rows of anterior teeth *adleri* (p. 439). 5
- One, or at most two, rows of anterior teeth 5
5. Buccal armature consists of large sharply pointed spike-like teeth; one or two rows of anterior punctiform teeth *clydei* (p. 445). 6.
- Buccal teeth either broad or narrow, straight and parallel, in palisade formation 6.
6. Buccal teeth about 18 *subtilis* (p. 447). 9.
- Buccal teeth about 40 *caffrarius* (p. 442). 9.
7. Pigmented area and buccal armature poorly developed, the latter with 4-6 widely spaced teeth *christophersi* and var. (p. 443). 8.
- Buccal armature and pigmented area well-developed, with more than 10 buccal teeth 8.
8. Buccal teeth less than 20 in number, sharply pointed, with points widely spaced *meillonii* (p. 446). 9.
- Buccal teeth 40 or more, straight, parallel, arranged in a palisade. 9.
9. Spermatheca with 8 segments; buccal teeth 40; pharyngeal armature well developed *affinis* and var. (p. 440). 10.
- Spermatheca with 10-12 segments; buccal teeth 50-60; pharyngeal armature inconspicuous 10.
10. Pigmented area with corrugated lines converging into the narrow anterior part *wansonii* (p. 451). 10.
- Pigmented area without such lines *thomsonii* (p. 449).

Key for the Males of the Subgenus *Sintonius*.

1. Males having both erect and recumbent hairs on abdominal tergites II-VI; buccal armature well-developed and with specific morphology; genitalia of the *Sergentomyia* type, usually with hooked paramere and pointed intromittent organ 2.
2. Palpal formula 1, 2, 4, 3, 5; anterior punctiform teeth present in buccal armature 3.
- Palpal formula 1, 2, 3, 4, 5; buccal armature without anterior punctiform teeth (except in *P. wansonii*) 6.
3. Only one row of anterior punctiform teeth in buccal cavity 4.
- Two or three rows of small anterior punctiform teeth *adleri* (p. 439). 4.
4. Buccal armature with 10 or more main teeth 5.
- Buccal armature with 2-5 main teeth *christophersi* and var. (p. 443). 5.
5. Buccal teeth arranged in groups of 3-6; six anterior denticles in an irregular row *clydei* (p. 445). 6.
- Buccal teeth not arranged in groups, anterior denticles in two lateral groups with small ones between. *subtilis* (p. 447). 6.
6. 10-12 punctiform teeth at the bases of the main teeth; anterior and posterior femora with spines *wansonii* (p. 451). 7.
- No anterior teeth in buccal cavity 7.
7. Four spines on style terminal *affinis* (p. 440). 8.
- Two of the four spines on style markedly subterminal, the other two being terminal 8.

8. Buccal armature has about 35 parallel teeth *thomsoni* (p. 449).
 Buccal armature has 10 broad teeth with serrated edges
meillonii and var. (p. 446).

Key for the Females of the Subgenus *Sergentomyia*.

- | | |
|---|-----|
| 1. Species with no erect hairs (except in <i>P. squamipleuris</i> on abdominal tergites II-VI. Buccal armature well developed and with specific morphology. Spermathecae not crenulated | 2. |
| 2. Well-marked notch in posterior border of buccal plate just anterior to buccal teeth <i>babu</i> (p. 478). | |
| No such notch present | 3. |
| 3. With spermathecae in the form of capsules or rounded sacs | 4. |
| With simple tubular spermathecae | 14. |
| 4. Spermathecae having a special shape, sac-like or turnip-shaped | 5. |
| Spermathecae elongate, cylindrical or elliptical capsules with smooth outline | 8. |
| 5. Spermathecae rounded or turnip-shaped; two well-developed lateral protuberances present anteriorly to the buccal armature | 6. |
| Spermathecae in the form of sacs; no lateral protuberances anteriorly to buccal armature | 7. |
| 6. Spermathecae bearing transverse rows of small spines; antennal formula 1/IV-XV <i>squamipleuris</i> and var. (p. 488). | |
| Spermathecae smooth without spines; antennal formula 2/III-XV <i>lewisi</i> (p. 493). | |
| 7. Spermathecae sac-like, with many fine parallel ridges <i>wurtzi</i> (p. 491). | |
| Spermatheca a thin-walled sac; buccal cavity with about 5 delicate pointed teeth <i>horgani</i> (p. 492). | |
| Spermatheca sac-like, constricted in the middle; buccal teeth 12-14 <i>mirabilis</i> (p. 497). | |
| 8. Spermathecae more or less cylindrical capsules with wide ducts | 9. |
| Spermathecae oval or elliptical capsules with narrow ducts | 11. |
| 9. Pharynx heavily armed, cordiform and pigmented; antennal formula 1/IV, 2/V-XV <i>simillimus</i> (p. 469). | |
| Pharynx not cordiform or heavily pigmented | 10. |
| 10. 10-12 equal and pointed teeth in buccal cavity, with a row of anterior punctiform teeth, each of which is placed at the interval between two teeth, pharynx three times as wide posteriorly as anteriorly <i>collarti</i> (p. 485). | |
| 12-14 unequal buccal teeth, the median ones much narrower than the lateral ones which are very wide; no anterior teeth; pharynx slender <i>decipiens</i> (p. 486). | |
| 22-24 pointed teeth in buccal cavity <i>kirki</i> (p. 483). | |
| 11. No large teeth in buccal cavity, only punctiform teeth <i>hunti</i> (p. 494). | |
| Large teeth present in buccal cavity | 12. |
| 12. Antennal formula 2/III-XV | 13. |
| Antennal formula 2/V-XIII, 1/XIV-XV <i>croasarai</i> (p. 479). | |
| 13. 10 pointed buccal teeth <i>yvonnae</i> (p. 480). | |
| 20-65 parallel buccal teeth, arranged in a palisade <i>freetownensis</i> and vars. (p. 472). | |
| 14. Pharynx cordiform <i>P. antennatus</i> and vars. (p. 452). | |
| Pharynx not cordiform | 15. |
| 15. Palpal formula 1, 2, 4, 3, 5 <i>lumsdeni</i> (p. 496). | |
| Palpal formula 1, 2, 3, 4, 5, ... | 16. |

16. Buccal armature with only one row of teeth 20.
Buccal armature with more than one row of teeth 17.
17. Posterior row of buccal armature with 30-45 teeth 18.
Posterior row of buccal armature with less than 15 teeth 19.
18. Median buccal teeth straight and narrow and forming a backwardly
projecting salient in the middle of the arc *ingrami* (p. 480).
Median buccal teeth not forming a salient *serratus* (p. 482).
19. Anterior buccal teeth comprising one row of 7 strong subconical teeth
notatus (p. 484).
Anterior buccal teeth comprising two rows of small punctiform teeth
having 16 and seven respectively *dureni* (p. 487).
20. Buccal teeth 50-60, equal and monomorphic 21.
Buccal teeth less than 40 22.
21. Buccal teeth about 50, very delicate and arranged in an arc deeply
concave posteriorly, the outer teeth directed outwardly
rutledgei (p. 495).
Buccal teeth 58-60, small and monomorphic, in palisade formation,
straight or only very slightly concave posteriorly . . . *renauzi* (p. 452).
22. Pharyngeal armature a series of transverse parallel lines, without true
teeth; buccal armature distinctive *schwetzi* (p. 470).
Pharyngeal armature with well-developed teeth 23.
23. $AI/III/E = \text{unity}$ *richardi* (p. 463).
 $AI/III/E < \text{unity}$ 24.
24. Ascid on IV < 0.5 length of segment . . . *schouedeni* and var. (p. 463).
Ascid on IV = or > 0.5 length of segment 25.
25. Buccal teeth equal and monomorphic 26.
Median buccal teeth smaller than lateral ones 27.
26. Buccal teeth 21 *pastorianus* (p. 466).
Buccal teeth about 25 *yusafi* (p. 465).
27. Buccal teeth 13-16, markedly unequal *buxtoni* (p. 467).
Buccal teeth 16-40 *bedfordi* and vars. (p. 458).

Key for the Males of the Subgenus *Sergentomyia*.

1. Males having teeth in the buccal cavity (except in *P. wurtzi*), and no
erect hairs on abdominal tergites II-VI (except sometimes in *P.*
squamipleuris) 2.
2. Style bearing more or less than 4 spines 3.
Style bearing 4 spines 4.
3. Style bearing only 2 spines *mirabilis* (p. 497).
Style bearing 7 spines *hirtus* (p. 496).
4. Buccal teeth vestigial or absent, pharynx unarmed 5.
Well marked buccal armature 6.
5. No teeth or pigmented area in buccal cavity *wurtzi* (p. 491).
Buccal teeth vestigial; pigmented area pear-shaped, narrow pos-
teriorly *horgani* (p. 492).
6. Penis sheath curved, finger-shaped, with blunt end 7.
Penis sheath conical and tapering 13.
7. Two of the spines on the style apical, the other two arise at 0.7
schwetzi (p. 470).
All four spines on style terminal or subterminal 8.
8. Third palpal segment as long as, or longer than, fourth segment
antennatus and vars. (p. 452).
Palpal formula 1, 2, 3, 4, 5 9.

9. Paramere as long, or nearly as long, as lateral lobe . . . *yusafi* (p. 465).
Paramere shorter than lateral lobe 10.
10. 24-40 teeth in buccal cavity 11.
Less than 20 teeth in buccal cavity 12.
11. Buccal cavity with 25 teeth, the outer 5 on each side broad and each
with several points, the central teeth narrow and pointed . . . *cowlandi* (p. 462).
Buccal cavity with 25-35 pointed teeth, median teeth only slightly
narrower than lateral ones *bedfordi* and vars. (p. 458).
12. About 14 teeth in buccal cavity, the lateral ones being larger than
median ones and pointing towards the centre; $AI/III < \text{unity}$. . . *buxtoni* (p. 467).
16-18 teeth in buccal cavity, the difference between the median and
lateral teeth not being marked; $AI/III > \text{unity}$. . . *schooutedeni* (p. 463).
13. Penis sheath tapering to a sharp point . . . *freetownensis* and vars. (p. 472).
Penis sheath tapering to a blunt point 14.
14. Paramere does not terminate in a beak 15.
Paramere with beaked extremity 18.
15. Two of the spines on style terminal; the other 2 at 0.5 16.
All 4 spines on style terminal or slightly subterminal 17.
16. Buccal teeth about 35, long, straight, narrow and pointed, with 2
irregular rows of anterior punctiform teeth . . . *serratus* (p. 482).
Buccal teeth about 30, small and rather irregular, and having a notch
about the centre *ingrami* (p. 480).
Buccal teeth about 21, very short and pointed, irregularly arranged
in 3 groups—one median, of 4 teeth, and two lateral, of 8-9 teeth . . . *kiriki* (p. 483).
17. $AI/III > \text{unity}$; pigmented area absent . . . *simillimus* (p. 409).
 $AI/III < \text{unity}$; buccal cavity with marked lateral protuberances
anterior to the buccal teeth; no ascoid on AI/III ; penis with dilated
end; wide scales on thoracic pleurae . . . *squamipleuris* and var. (p. 488).
18. Pigmented area absent 19.
Pigmented area present 20.
19. Buccal teeth 8-10; pharynx unarmed *dureni* (p. 487).
Buccal teeth 10-12, with an anterior row of small punctiform teeth;
pharynx armed with fine transverse lines . . . *collarti* (p. 485).
20. No posterior row of large pointed teeth in buccal armature . . . *hunti* (p. 494).
Posterior row of buccal teeth either the only row in the buccal cavity
or very large and prominent compared with anterior punctiform
ones 21.
21. Buccal teeth 12-14, markedly unequal, the 4-5 median teeth being
pointed and narrower than the lateral ones (as in the female of the
same species) *decipiens* (p. 486).
Buccal teeth 18-20, not markedly unequal 22.
22. Buccal cavity rather resembling that of *P. antennatus* var. *signati-*
pennis, with a row of small anterior teeth . . . *babu* (p. 478).
No anterior teeth; buccal teeth broad, irregular in contour, and
finely crenulated (like the lateral teeth in *P. cowlandi*) . . . *aretasi* (p. 468).

IV. DESCRIPTIONS OF THE ETHIOPIAN SPECIES.

Phlebotomus (Phlebotomus) papatasi Scopoli.*Bibio papatasi* Scopoli, 1786, *Deliciae faunae et flora insubricae* 1: 55.*Musca papatasi* Gmelin, 1788-93, In *Linnaei Systema Naturae*, Edit. 13.

Flebotomus papatasi Rondani, 1840, *Memoria prima per Serv. alla Ditterologia Ital.*, Parma, XIII.

Cynipes molesta Costa, 1843, *Ann. Accad. aspir. Nat.* 1: 4.

Haemasson minutus Loew, 1884, *Stettin. ent. Ztg.* 5: 115.

Hebotomus papatasi Rondani, 1843, *Ann. Soc. ent. Fr.* (2) 1: 265.

Phlebotomus papatasi Loew, 1847, *Stettin. ent. Ztg.* 8: 140.

The early synonymy of this species has given rise to much discussion (for details see Sinton, 1928 and Theodor, 1948) which is now principally of historical interest, since the name *Phlebotomus papatasi* has been included in a list of *nomina conservanda* as quoted by Handlirsch (1925) in Schröder's *Handbuch der Entomologie*, 3: 91. The descriptions below are from Sudan specimens of this insect, 10 males and 10 females.

♀. Length: 3-3.1 mm. Antenna: formula 2/III-XV, segment III (0.24-0.30 mm.) > IV + V, AIII/E = 0.67-1, ascoids on IV = 0.5 length of segment. Palp: formula 1, 4, 2, 3, 5, relative lengths 1, 3.6, 4.4, 3.0, 7. Epipharynx: length 0.3-0.4 mm. Pharynx:

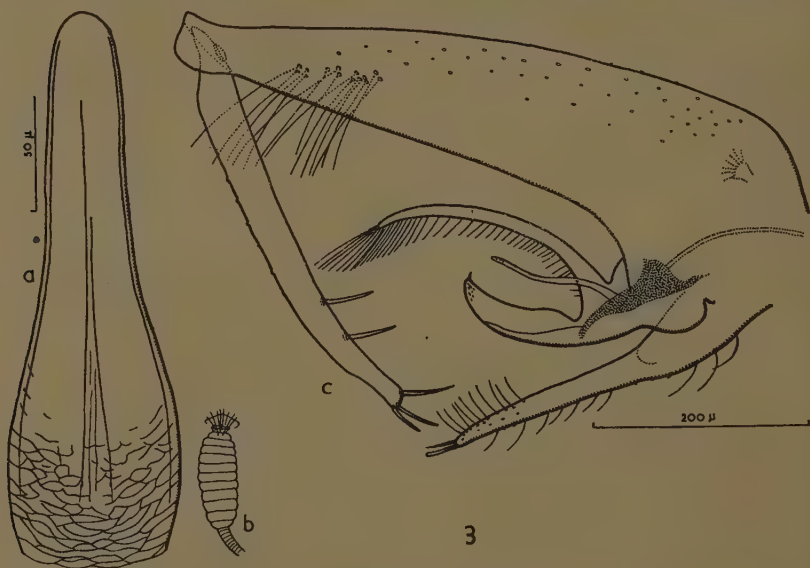


FIG. 3.—*P. papatasi*, ♀: a, pharynx; b, spermatheca. ♂: c, terminalia (a after Adler and Theodor, 1926; b, from Sudan specimen; c after Parrot and Gougis, 1944).

about twice as wide posteriorly as anteriorly, armature a network of fine wavy lines among which can be seen backwardly projecting teeth. Wing: length 2.0-2.4 mm., width 0.56-0.63 mm., alar index 1.3-1.8, delta + 0.1 to + 0.15 mm. Spermatheca: with about 10 segments, the "head" is large and broad with no distinct neck, segments decrease in size towards the duct which is irregularly annulated and opens separately into the vulva.

♂. Length: 2.6 mm. Antenna: formula 2/III-XV, segment III (0.27-0.34 mm.) > IV + V, AIII/E = 1.1-1.25, ascoids on IV = 0.25 length of segment. Palp: formula 1, (2, 4), 3, 5, relative lengths 1, 3.6, 5.0, 3.6, 7.2. Epipharynx: length 0.23-0.27 mm.

Pharynx : slightly less than twice as wide posteriorly as anteriorly armed with scale-like spines and ridges with punctiform small teeth. *Wing* : length 1.8–2.1 mm., width 0.48–0.53 mm., alar index 1.2–1.4, delta + 0.08 to + 0.09 mm. *Terminalia* : coxite (0.55–0.60 mm.) 1.4 times as long as style (0.37–0.41 mm.), which bears five short spatulate spines, three terminal and two submedian, the distance between the two submedian spines being much less than that between the distal submedian spine and the end of the segment; paramere (0.28–0.37 mm.) three-lobed owing to the presence of two dorsal processes, the sickle-shaped fimbriated process, bearing many hairs, and the straight digitiform process which in *P. papatasi* is much shorter than the fimbriated process; penis sheath (0.15 mm.) roughly conical with extremity curved downwards; lateral lobe (0.35–0.4 mm.) with two long terminal bristles.

Distribution : A.-E. SUDAN, SOMALILAND, FRENCH WEST AFRICA. Also widely distributed in the MEDITERRANEAN area and WESTERN ASIA.

Phlebotomus (Phlebotomus) papatasi var. *bergeroti* Parrot.

P. papatasi var. *bergeroti* Parrot, 1934, *Arch. Inst. Pasteur Algér.* 12 : 383.

P. viduus Parrot, 1936, *ibid.* 14 : 39.

P. papatasi var. *bergeroti* Parrot, 1941, *ibid.* 19 : 437.

Type locality Djanet (Tassili des Ajjers), Central Sahara. The descriptions below are after Parrot (1934, 1940) from 4 males and 19 females. Type specimens in the Institut Pasteur d'Algérie.

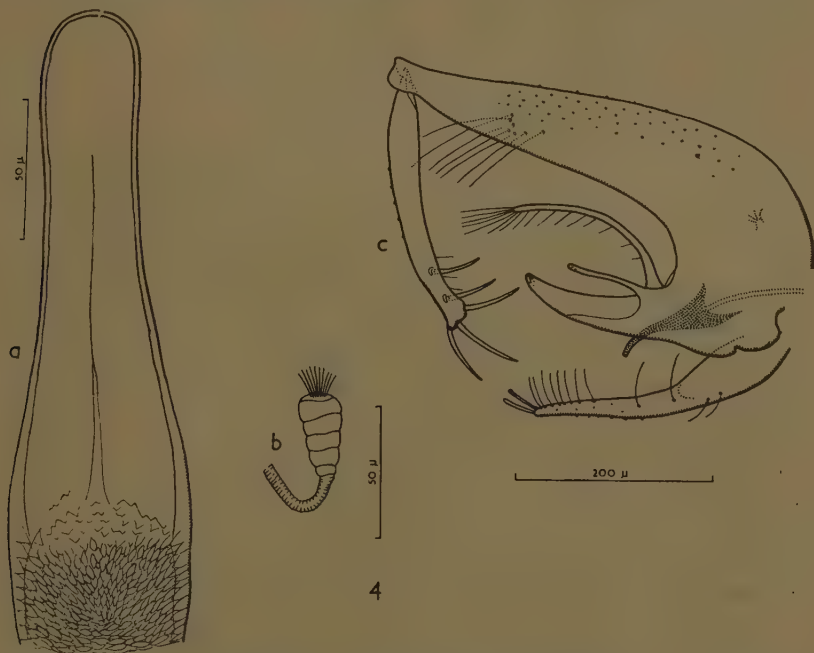


FIG. 4.—*P. papatasi* var. *bergeroti*, ♀; a, pharynx; b, spermatheca. ♂: c, terminalia. (a and b after Parrot, 1936; c after Parrot, 1944.)

♀. *Length*: 2.4–2.7 mm., hind leg 3.7–3.8 mm. *Antenna*: formula 2/III–XV, segment III (0.22–0.44 mm.) > IV + V, AIII/E = 0.65–0.76, ascoids on IV = 0.75 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 3, 4, 2.8, 7. *Epipharynx*: length 0.3–0.35 mm. *Pharynx*: twice as wide posteriorly as anteriorly and armed with numerous broad scale-like teeth resembling those in the *sergenti* group, and pointing obliquely towards the mid-line. *Wing*: length 2.18–2.25 mm., width 0.6–0.65 mm., alar index 1.3–1.4, delta + 0.09 to + 0.11 mm. *Spermatheca*: with 5–8 segments, decreasing in size towards the duct, which is irregularly annulated and opens separately into the vulva.

♂. *Length*: 2.4–2.9 mm., hind leg 3.7 mm. *Antenna*: formula 2/III–XV, segment III (0.24–0.28 mm.) > IV + V, AIII/E = 1–1.1, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 3.4, 5.2, 3.7, 7.6. *Epipharynx*: length 0.22–0.24 mm. *Pharynx*: as in *P. papatasi*, with the ridges more accentuated. *Wing*: length 1.8–2 mm., width 0.44–0.53 mm., alar index 1.3–1.6, delta + 0.05 to + 0.09 mm. *Terminalia*: coxite (0.37 mm.) 1.4 times as long as style, with a tuft of 6–7 long hairs distally on its internal surface; style bears five spatulate spines, three terminal and two submedian, the more distal of the latter two arising midway between the apex of the segment and the proximal submedian spine; paramere three-lobed as in *P. papatasi*, penis sheath conical, lateral lobe with two relatively long spatulate terminal bristles.

The male of var. *bergeroti* differs from the typical *P. papatasi* in the greater length of AIII, the smaller tuft of hairs on the coxite, and the position of the submedian spines on the style. The female is differentiated by the greater length of the ascoids, the more heavily armed pharynx and the spermatheca, with 5–8 segments only.

Distribution: CENTRAL SAHARA, ABYSSINIA, A.-E. SUDAN.

Phlebotomus (Phlebotomus) roubaudi Newstead.

P. roubaudi Newstead, 1913, *Bull. Soc. Path. exot.* 6: 124.

P. duboscqi Franca & Parrot, 1921, *Arch. Inst. Pasteur Afr. N.* 1: 283.

P. roubaudi Parrot & Gougis, 1944, *Arch. Inst. Pasteur Alger.* 22: 40.

This species was described by Newstead (1913) from specimens collected in the region from which the type specimens of *P. duboscqi* Neveu-Lemaire were obtained. Although showing specific characters, *P. roubaudi* resembles *P. papatasi* closely, and Newstead pointed out that it might be identical with *P. duboscqi*, the species created but imperfectly described by Neveu-Lemaire in 1906. Detailed descriptions of both sexes of *P. roubaudi* were published in 1944 by Parrot and Gougis who consider that, as the name *P. roubaudi* refers to an adequately described form, it should be regarded as correct until the matter can be settled by re-examination of the type specimens of *P. duboscqi*. The description below is taken from Parrot and Gougis. Type specimen is in the British Museum.

♀. *Length*: 2.25 mm. *Antenna*: formula 2/III–XV, segment III (0.3 mm.) = IV + V, AIII/E = 0.8, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 3.1, 3.6, 2.5, —. *Epipharynx*: length 0.37 mm. *Pharynx*: posterior width about twice anterior width, bearing numerous scale-like teeth. *Wing*: length 1.9 mm., width 0.67 mm., alar index 1.35, delta + 0.14 mm. *Spermatheca*: of *papatasi* type, with 8 segments decreasing in size from the terminal one; ducts narrow, irregularly annulated and opening separately into the vulva.

♂. *Length*: 2.3 mm. *Antenna*: formula 2/III–XV, segment III (0.26 mm.) < IV + V, AIII/E = 1, ascoids on IV = 0.3 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.8, 3.9, 3.2, 7. *Epipharynx*: length 0.25–0.26 mm. *Pharynx*: less than twice as wide posteriorly as anteriorly and armed with numerous scale-like spines, mostly pointed

or appearing as wavy lines with some punctiform denticulations. *Wing*: length 1.83–1.88 mm., width 0.43–0.5 mm., alar index 1.2–1.6, delta + 0.034 to 0.1 mm., pi + 0.05 to + 0.085 mm. *Terminalia*: coxite (0.54–0.63 mm.) about half as long as the abdomen, bearing on the anterior part of its inner surface a small process with short hairs and on its posterior part about 12 long hairs; style (0.42–0.48 mm.) bears five short, strong, spatulate spines, three apical and two internal submedian ones, the most distal of which is equidistant between the apex of the segment and the most proximal spine (compare with *P.*

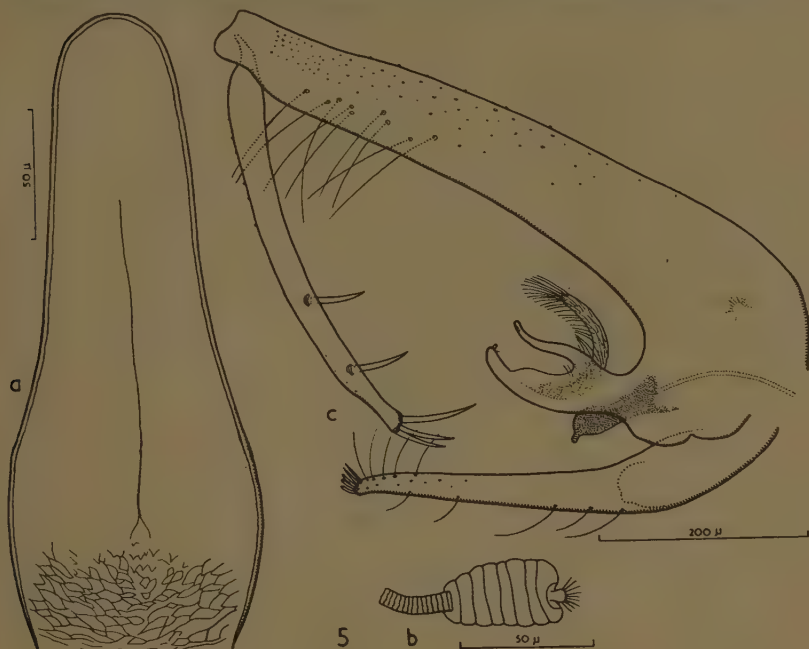


FIG. 5.—*P. roubaudi*, ♀: *a*, pharynx; *b*, spermatheca. ♂: *c*, terminalia. (After Parrot and Gougis, 1944.)

papatasi); paramere (0.27–0.29 mm.) three-lobed, fimbriated process completely covered with hairs and not much longer than digitiform process; penis (0.12 mm.) of irregular shape, lateral lobe (0.38–0.4 mm.) shorter than coxite and armed at its tip with 5 or more short strong spatulate spines.

Distribution: ASHANTI, FRENCH SUDAN, A.-E. SUDAN, NIGERIA, SIERRA LEONE, FRENCH NIGER.

Phlebotomus (Phlebotomus) roubaudi var. *fourtoni* Floch & Abonnenc.

P. roubaudi var. *fourtoni* Floch & Abonnenc, 1948, *Inst. Pasteur Guyane Territoire de l'Inini*, Publ. 169 (Cayenne).

Type specimens in the Institut Pasteur at Cayenne. The description below is after Floch and Abonnenc, from two males.

♀. Unknown.

♂. *Length*: 3.3 mm. *Antennæ*: formula 2/III-XV, segment III (0.296 mm.) < IV + V, AIII/E = 1.1, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 4, 5.2, 4.4, 10.2. *Epipharynx*: length 0.25 mm. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with numerous coarse, irregularly arranged teeth. *Wing*: length 1.94 mm., width 0.48 mm., alar index 1.7, delta + 0.09 mm. *Terminalia*: coxite (0.63 mm.) has on its inner surface a small tubercle bearing two long bristles and several short hairs; style (0.47 mm.) bearing five relatively short spines, three terminal,

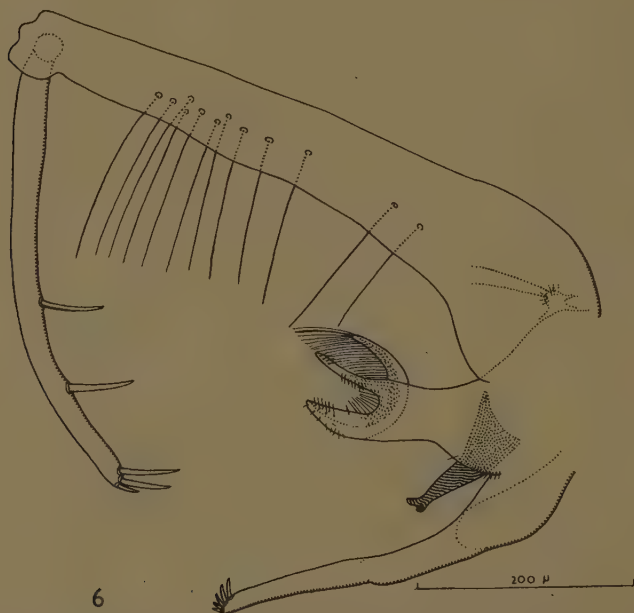


FIG. 6.—*P. roubaudi* var. *fourtoni*, ♂: terminalia (after Floch and Abonnenc, 1948).

a proximal one arising slightly below the middle of the segment, and the fifth one equidistant between the proximal spine and the terminal ones; paramere (0.259 mm.) three-lobed as in *P. roubaudi*; penis sheath (0.11 mm.) with wide base, tapering progressively until just before the dilated extremity, the whole organ having roughly the shape of a boot; lateral lobe 0.41 mm.

The male of this variety differs from *P. roubaudi* in (1) its greater length, (2) the boot-shaped penis sheath, and (3) the presence of two long bristles and several short hairs on the tubercle of the coxite; in *P. roubaudi* there are only short hairs.

Distribution: FRENCH SUDAN.

Phlebotomus (Phlebotomus) duboscqi Neveu-Lemaire.*P. duboscqi* Neveu-Lemaire, 1906, *Bull. Soc. zool. Fr.* 31 : 65.*P. duboscqi* Picard, 1909, *Bull. Soc. ent. Fr.* 1909 : 164.

Type locality Timbuctoo. This species was created by Neveu-Lemaire in 1906, but the description of it is deficient in essential characters. Picard (1909), who re-examined the type specimen states that he was unable to distinguish any difference between it and *P. papatasi*. The status of the species is uncertain at present and re-examination of the type specimens is required to determine its relation to *P. roubaudi*, *P. papatasi* and *P. papatasi* var. *bergeroti*.

Distribution : FRENCH WEST AFRICA.

Phlebotomus (Phlebotomus) alexandri Sinton.*P. sergenti* var. Newstead, 1920, *Bull. ent. Res.* 11 : 305.*P. sergenti* var. *alexandri* Sinton, 1928, *Indian J. med. Res.* 16 : 297.*P. alexandri* Parrot, 1936, *Arch. Inst. Pasteur Algér.* 14 : 428.

Type locality Amara, Mesopotamia ; type specimen in the British Museum. The description of the female given below is mainly after Parrot (1936), that of the male from a specimen from the A.-E. Sudan.

♀. *Length* : 2.22 mm., hind leg 2.8-3.1 mm. *Antenna* : formula 2/III-XV, segment III (0.14-0.16 mm.) < IV + V, AIII/E = 0.58-0.62, ascoids on IV = 0.5 length of segment. *Palp* : formula 1,4,2,3,5, relative lengths 1, 2.7, 3.6, 2.2, 4.4. *Epipharynx* : length



FIG. 7.—*P. alexandri* ♂ : terminalia.

0.22-0.26 mm. *Pharynx* : twice as wide posteriorly as anteriorly, armed with numerous broad pointed leaf-like teeth directed obliquely medially and posteriorly. *Wing* : length 1.85-2 mm., width 0.48-0.51 mm., alar index 1.3-1.5, delta + 0.05 to + 0.07 mm. *Spermatheca* : with 7-8 segments, the terminal one appearing detached from the others ; ducts wide at their origin becoming narrower and opening separately into the vulva.

♂. *Length* : 2.1 mm., hind leg 2.5 mm. *Antenna* : formula 2/III-XV, segment III < or = IV + V, AIII/E = 0.7-1.1, ascoids on IV = 0.4 length of segment. *Palp* : formula 1,2,4,3,5, or 1, (2,4), 3,5. *Pharynx* : less than twice as wide posteriorly as anteriorly and armed with irregular, fine, scale-like ridges. *Wing* : length 2.0 mm., width 0.56 mm., alar index 1.3, delta + 0.08 mm. *Terminalia* : coxite (0.21 mm.) less than twice length

of style and bearing a tuft of straight, rigid, divergent hairs on a short rounded process on its inner surface; style (0.15 mm.) bears four spines, two submedian, one terminal and one subterminal, the distal, bifurcated spine bearing process of the segment markedly unequal, the terminal branch being about three times the length of the other; paramere 0.2 mm., penis sheath 0.09 mm., lateral lobe (0.24-0.26 mm.) longer than coxite.

Distribution: A.-E. SUDAN.

Phlebotomus (Phlebotomus) sergenti Parrot.

P. sergenti Parrot, 1917, *Bull. Soc. Path. exot.* 10: 564.

P. sergenti Franca, 1918, *ibid.* 11: 731.

P. sergenti Adler & Theodor, 1929, *Ann. trop. Med. Parasit.* 23: 271.

Type locality MacMahon (Constantine), Algiers; type specimen in the Institut Pasteur d'Algérie. The description of the male is after Parrot (1917) and Newstead (1920), that of the female mainly after Franca (1918) and Adler and Theodor (1929).

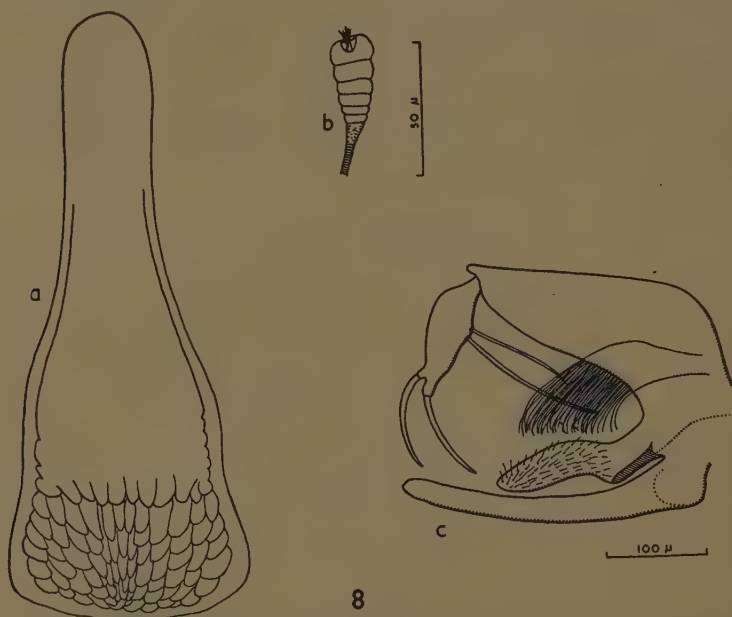


FIG. 8.—*P. sergenti*, ♀: a, pharynx; b, spermatheca. ♂: c, terminalia. (a and b after Adler & Theodor, 1929; c after Newstead, 1920.)

♀. Length: 1.6-3.0 mm. Antenna: formula 2/III-XV, segment III (0.27-0.3 mm.) > IV + V, AIII/E = 0.68-0.88, ascoids on IV = 0.5 length of segment. Palp: formula 1,4,2,3,5 (often variable). Epipharynx: length 0.32-0.44 mm. Pharynx: about 2.5 times as wide posteriorly as anteriorly and armed with very characteristic broad scale-like teeth. Wing: length 2.5 mm., width 0.8 mm., alar index 1, delta + 0.08 mm. Spermatheca: with 4-6 segments, superior segment longer than others, which diminish in size from above downwards; the "head" is small and carried on a short neck partly

invaginated into the first segment; ducts enter the vulva separately and widen considerably at their junction with the body of the spermatheca.

♂. *Length*: 2-3.2 mm. *Antenna*: formula 2/III-XV, segment III (0.25 mm.) = IV + V, AIII/E = 1-1.4, ascoids on IV = 0.3 length of segment. *Palp*: formula 1,(4,2), 3,5, relative lengths 1, 4.2, 5, 4.2, 8.5. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with broad leaf-like teeth, but those on the dorsal plate are poorly developed and hence appear separate from those on the lateral plates which appear conspicuous anteriorly. *Wing*: length 1.9 mm., width 0.53 mm., alar index 1.23, delta + 0.07 mm. *Terminalia*: coxite (0.25 mm.) more than twice as long as style (0.11 mm.), which appears almost globular; coxite bears near its base on inner surface a peduncle with rounded extremity, from which arises a tuft of about a dozen hairs; style bears four spines, two terminal on a separate process and two submedian; paramere (0.15 mm.) single, with flat elliptical upper surface; penis sheath (0.06 mm.) short with terminal hook; lateral lobe 0.13 mm.

Distribution: AIR (ASBEN) IN CENTRAL SAHARA, FRENCH WEST AFRICA; also in MEDITERRANEAN AREA and in ASIA.

Phlebotomus (Phlebotomus) sergenti var. *saevus* Parrot & Martin.

P. sergenti var. *saevus* Parrot & Martin, 1939, *Arch. Inst. Pasteur Algér.* 17: 484.

Type locality Aouache, Abyssinia; type specimens in the Institut Pasteur d'Algérie. The descriptions below are mainly after Parrot and Martin, from two males and five females.

♀. *Length*: 2.26 mm., hind leg 2.55-3.95 mm. *Antenna*: formula 2/III-XV, segment III (0.22 mm.) > IV + V, AIII/E = 0.7-0.75, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 2.8, 4.1, 2.7, 7.1. *Epipharynx*: length 0.28-

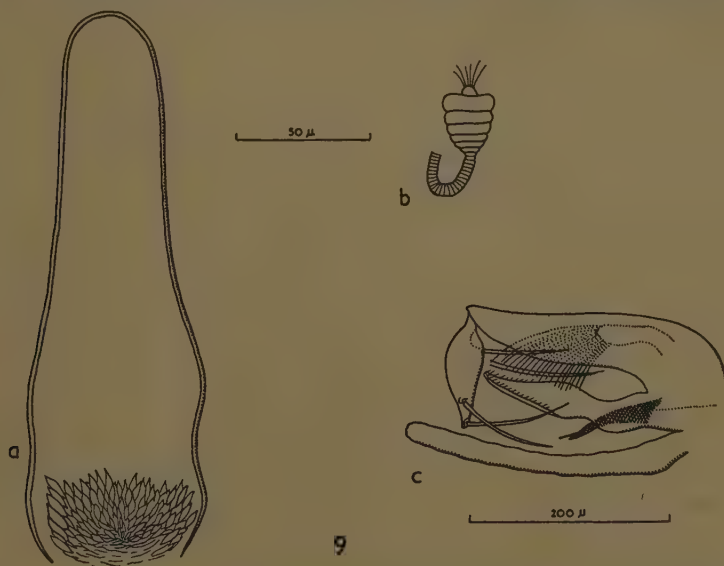


FIG. 9.—*P. sergenti* var. *saevus*, ♀: a, pharynx; b, spermatheca. ♂: c, terminalia. (after Parrot and Martin, 1939.)

0.3 mm. *Pharynx*: less than twice as wide posteriorly as anteriorly, constricted in posterior part which bears numerous broad, scale-like teeth. *Wing*: length 2.1–2.4 mm., width 0.57–0.65 mm., alar index 1.2–1.4, delta + 0.21 to 0.13 mm. *Spermatheca*: with 6 segments, distal one larger than the others; ducts open separately into the vulva.

♂. *Length*: 2.49 mm., hind leg 4.8 mm. *Antenna*: formula 2/III–XV, segment III (0.32 mm.) = IV + V, AIII/E = 1.06, ascoids on IV = 0.7 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 3.2, 4, 3.1, 6. *Epipharynx*: length 0.39 mm. *Pharynx*: less than twice as wide posteriorly as anteriorly, traversed in its posterior part by irregularly arranged scale-like folds. *Wing*: length 2.49 mm., width 0.65 mm., alar index 1.26, delta + 0.08 mm. *Terminalia*: coxite (0.26 mm.) more than twice length of style (0.12 mm.) and having on its inner surface a tuft of about 25 long curved hairs, arising from an elongated process (0.08 mm. approximately); style with four spines as in *P. sergenti*, but one of the two distal spines is terminal and the other subterminal (as in *P. alexandri*).

The male of var. *saevus* differs from *P. sergenti* in (1) the general arrangement of the tuft of hairs on the coxite, (2) the shape of the process bearing these hairs and (3) the arrangement of the terminal spines on the style. The female differs from *P. sergenti* in its greater length and the more numerous but less well-developed teeth in the pharyngeal armature.

Distribution: ABYSSINIA, A.-E. SUDAN.

Phlebotomus (Phlebotomus) katangensis Bequaert & Walravens.

P. katangensis Bequaert & Walravens, 1930, *Rev. Zool. Bot. afr.* 19: 35.

Type locality Elizabethville, Katanga, Belgian Congo. The description of the male is after Bequaert and Walravens.

♀. Unknown.

♂. *Length* (thorax to tip of style): 2.2–2.6 mm. *Antenna*: formula 2/III–IX, I/X..., segment III > IV + V, AIII/E = 0.6. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 2.4,

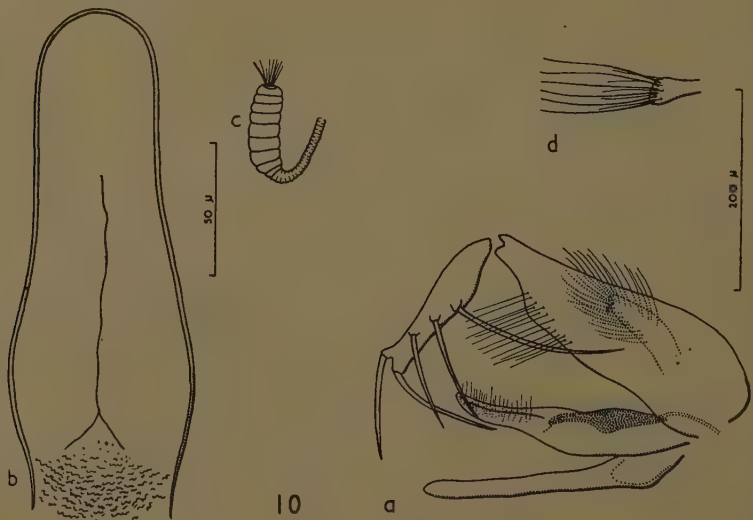


FIG. 10.—*P. katangensis*, ♂: a, terminalia. *P. martini*, ♀: b, pharynx; c, spermatheca. ♂: d, lobe of coxite. (a after Bequaert and Walravens, 1930; b–d after Parrot, 1936.)

2.7, 2.7, 5.7. *Epipharynx*: length 0.21–0.22 mm. *Pharynx*: about 1.5 times as wide posteriorly as anteriorly, armed with irregular transverse ridges bearing small spines. *Wing*: length 1.8–2 mm., width 0.46–0.6 mm., alar index 1.7–2, delta + 0.1 to + 0.18 mm. *Terminalia*: coxite (0.28 mm.) about twice as long as style (0.15 mm.) and having on a process about the middle of its internal surface a tuft of long hairs; style bears five spines two terminal and three lateral, of which two arise on the distal half of the segment and one on its proximal half, this spine being notably longer than the others; paramere (0.2 mm.) blunt; penis sheath (0.1 mm.) slender, curved slightly downwards with blunt points; lateral lobe 0.23 mm.

Distribution: BELGIAN CONGO.

Phlebotomus (Phlebotomus) martini Parrot.

P. martini Parrot, 1936, *Arch. Inst. Pasteur Algér.* 14: 30.

Type locality Addis Ababa, Abyssinia; type specimens in the Institut Pasteur d'Algérie. The descriptions given below, after Parrot, from two males and nine females, agree with specimens from the A–E Sudan.

♀. *Length*: 2.2 mm., hind leg 3–3.7 mm. *Antenna*: formula 2/III–XV, segment III (0.18–0.23 mm.) > or = IV + V, AIII/E = 0.68–0.93, ascoids on IV = 0.7 length of segment. *Palp*: formula 1,(4,2),3,5, relative lengths 1, 3.5, 3.9, 3.4, 7.0. *Epipharynx*: length 0.25–0.3 mm. *Pharynx*: about 1.5 times as wide posteriorly as anteriorly, armed with irregular transverse ridges and punctiform teeth. *Wing*: length 1.8–2.4 mm., width 0.53–0.64 mm., alar index 1.2–1.5, delta + 0.09 to + 0.11 mm. *Spermatheca*: with 9–10 segments, no neck but terminating in a tuft of hairs; ducts narrow, irregularly annulated and opening separately into the vulva.

♂. *Length*: 1.8–2 mm., hind leg 2.8–2.9 mm. *Antenna*: formula 2/III–X, I/XI–XIII, segment III (0.18–0.19 mm.) < IV + V, AIII/E = 0.9, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 3.1, 4, 3.6, 7.4. *Epipharynx*: length 0.2 mm. *Pharynx*: 1.5 times as wide posteriorly as anteriorly, armed with fine wavy ridges and small punctiform teeth. *Wing*: length 1.6–1.7 mm., width 0.48–0.49 mm., alar index 1.3–1.5, delta + 0.05 to + 0.07 mm. *Terminalia*: coxite (0.27 mm.) more than twice length of style (0.13 mm.) and bearing on its inner surface a process from which arise six long flattened hairs and about 12 small, short, slender ones; style bears five spines, two submedian, one subterminal and two terminal; paramere (0.18 mm.) with blunt extremity; penis sheath 0.07 mm., lateral lobe (0.23 mm.) shorter than coxite.

P. katangensis, *P. martini* and *P. rossi* form a small group (*Synphlebotomus* of Theodor, 1948) distinguished by the prominent tuft of hairs on the coxite and five spines on the style in the male terminalia. The males of *P. katangensis* and *P. martini* are very similar, differing only in the character of the hairs on the process of the coxite. These hairs are described as of uniform size in *P. katangensis*, whereas in *P. martini* there are small as well as large hairs, although the small hairs are very inconspicuous and might easily be overlooked. It is possible that the two species are identical, in which case *P. martini* would become a synonym of *P. katangensis*; but this can only be decided by re-examination of the type specimen of *P. katangensis*.

Distribution: ABYSSINIA, A.–E. SUDAN.

Phlebotomus (Phlebotomus) rossi De Meillon & Lavoipierre.

P. rossi De Meillon & Lavoipierre, 1944, *J. ent. Soc. S. Afr.* 7: 44.

Type specimen in the South African Institute for Medical Research, Johannesburg. This species is known from one male only, from Raheen,

Umtali, Southern Rhodesia description of which is given after De Meillon and Lavoipierre.

♀. Unknown.

♂. Length: 2.6 mm. Antenna: formula 2/III-IX, I/X-XIII, 0/XIV-XV, segment III (0.24 mm.) = IV + V, AIII/E = 1.2, ascoids on IV = 0.5 length of segment. Palp: formula 1,2,(3,4),5, relative lengths 1,3,4,4,9.5. Epipharynx: length 0.2 mm. Pharynx: 1.5 times as wide posteriorly as anteriorly, armed with irregular ridges and punctiform teeth. Wing: length 2.0 mm., width 0.6 mm., alar index 1.4 delta + 0.14 mm. Terminalia: coxite (0.3 mm.) about twice as long as style (0.16 mm.) and bearing a process with about four very long bristles apically and a large number of shorter hooked bristles

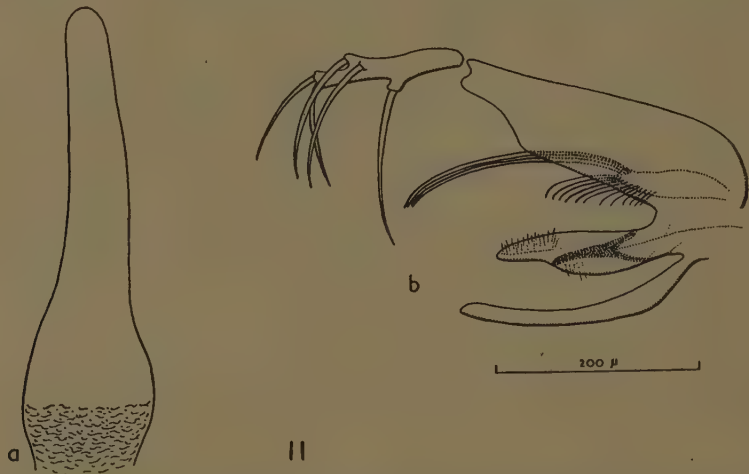


FIG. 11.—*P. rossi*, ♂: a, pharynx; b, terminalia. (After De Meillon and Lavoipierre, 1944.)

ventrally decreasing in size from near the apex to the base; style bears five long spines, two terminal, two subterminal and one submedian, which is the longest of the five; paramere (0.18 mm.) evenly rounded distally, penis sheath (0.1 mm.) with rounded distal end; lateral lobe 0.26 mm.

The male of this species resembles those of *P. katangensis* and *P. martini*, from which it is distinguished by the character of the setae on the coxite.

Distribution: SOUTHERN RHODESIA.

Phlebotomus (Phlebotomus) orientalis Parrot.

P. langeroni var. *orientalis* Parrot, 1936, *Arch. Inst. Pasteur Algér.* 14: 30.

P. perniciosus Archibald & Mansour, 1937, *Trans. R. Soc. trop. Med. Hyg.* 30: 395.

P. perniciosus Sinton, 1937, *ibid.* 30: 404.

P. perniciosus Kirk, 1939, *ibid.* 32: 541.

P. langeroni Theodor, 1938, *Bull. ent. Res.* 29: 165.

P. orientalis Parrot & Clastrier, 1946, *Arch. Inst. Pasteur Algér.* 24: 60.

P. langeroni was separated as a variety of *P. perniciosus* by Nitzulescu (1930) on the characters of a non-bifid penis sheath and a different antennal

formula and was later raised to specific rank by the same author. In 1936 Parrot described from Abyssinia *P. langeroni* var. *orientalis*, in which the penis is non-bifid but the antennal formula is similar to that of *P. perniciosus*. The specimen reported by Theodor (1938) from the Sudan as *P. langeroni* was probably var. *orientalis*, but as the antennae were missing this could not be decided. In a study of *P. langeroni* and allied forms, Parrot and Clastrier (1946) concluded that *P. langeroni* differed as much from the variety *orientalis* as from two allied species, *P. longipes* and *P. longicuspis*, and accordingly raised the variety to specific rank as *P. orientalis* Parrot, 1936.

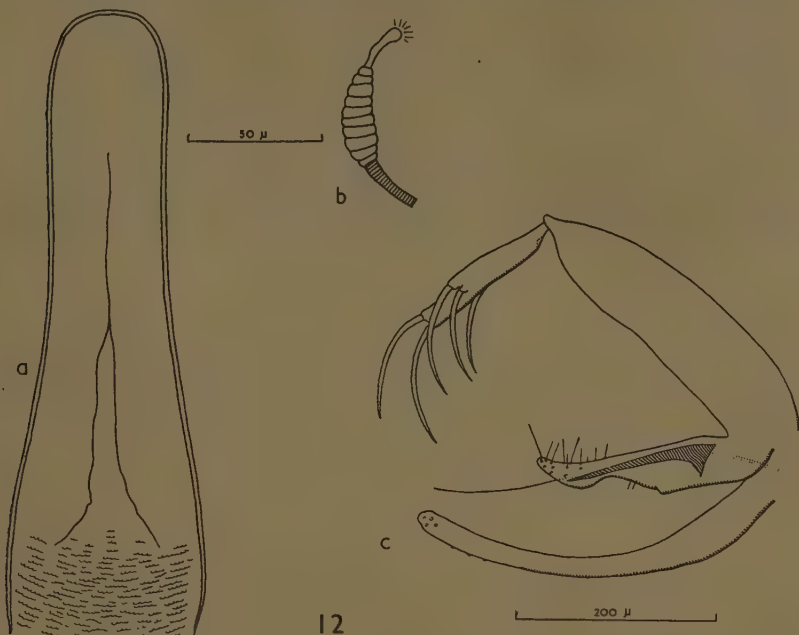


FIG. 12.—*P. orientalis*, ♀: a, pharynx; b, spermatheca. ♂: c, terminalia. (After Parrot, 1936.)

Type locality Dira Dawa, Abyssinia; type specimens in the Institut Pasteur d'Algérie. The descriptions below are mainly after Parrot's (1936) descriptions of 32 males and 24 females from the type locality which agree with specimens from the A.-E. Sudan.

♀. *Length*: 2.25 mm., hind leg 3.7–4.3 mm. *Antenna*: formula 2/III–XV, segment III (0.25–0.3 mm.) > IV + V, AIII/E = 0.96–1, ascoids on IV = 0.3 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 3.5, 4.3, 3.3, 8. *Epipharynx*: length 0.26–0.32 mm. *Pharynx*: less than twice as wide posteriorly as anteriorly and armed with transverse rows of fine punctiform teeth. *Wing*: length 1.9–2.5 mm., width 0.6–0.75 mm., alar index 1.6–1.8, delta + 0.11 to + 0.18 mm. *Spermatheca*: with long "neck" and 8–12 segments; ducts annulated and of uniform diameter for two-thirds of their

length, but smooth and widening progressively in the terminal third, opening separately into the vulva.

♂. *Length*: 2-2.3 mm., hind leg 3.2-3.8 mm. *Antenna*: formula 2/III-VII (VIII), 1/VIII (IX)-XV, segment III (0.25-0.32 mm.) $> IV + V$, AIII/E = 1.2-1.3, ascoids on IV = 0.2 length of segment. *Palp*: formula 1,4,2,3,5, relative lengths 1, 3.4, 4, 3.3, 8. *Epipharynx*: length 0.2-0.25 mm. *Pharynx*: almost twice as wide posteriorly as anteriorly, armed with fine punctiform teeth. *Wing*: length 1.4-1.6 mm., width 0.46-0.6 mm., alar index 1.5-2.25, delta + 0.07 to + 0.18 mm. *Terminalia*: coxite (0.29-0.35 mm.) approximately twice length of style (0.14-0.17 mm.) which bears five spines, two terminal, one submedian and external, and two internal ones arising nearer to the submedian external spine than to the terminal spines; paramere (0.2-0.23 mm.) slightly upturned at apex; penis sheath (0.14-0.17 mm.) narrow and elongated, ending in a single point, infero-external; lateral lobe (0.3-0.37 mm.) as long as or longer than coxite.

Distribution: ABYSSINIA, A.-E. SUDAN, NORTHERN KENYA.

Phlebotomus (Phlebotomus) longipes Parrot & Martin.

P. longipes Parrot & Martin, 1939, *Arch. Inst. Pasteur Algér.* 17: 143.

Type locality Addis Ababa; type specimens in the Institut Pasteur d'Algérie. The descriptions given below are after Parrot and Martin from 896

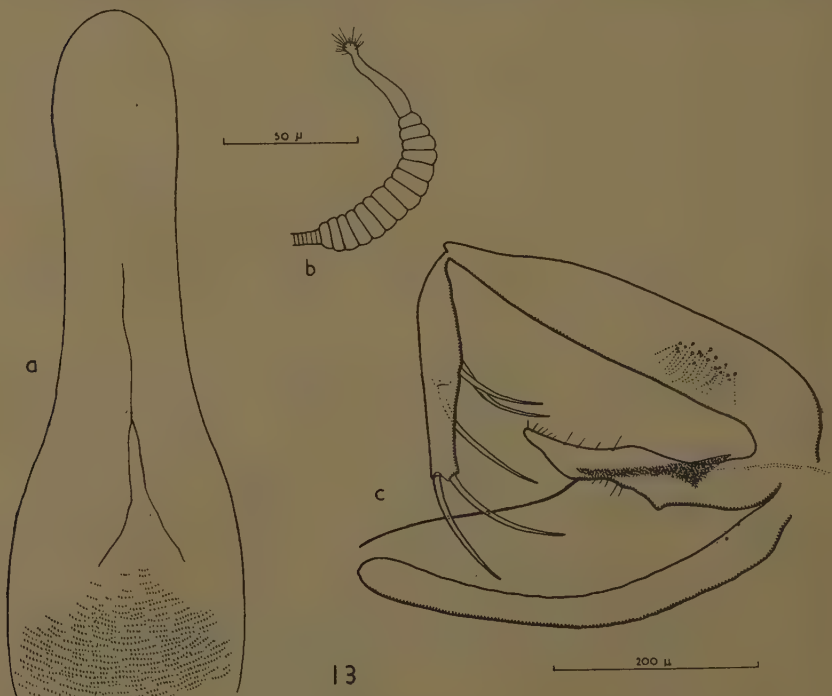


FIG. 13.—*P. longipes*, ♀: a, pharynx; b, spermatheca. ♂: c, terminalia. (After Parrot and Martin, 1939.)

males and 642 females from Abyssinia and agree with specimens from the Sudan.

♀. Length: 2.76-3 mm., hind leg 5.32-5.83 mm. Antenna: formula 2/III-XV, segment III (0.4-0.44 mm.) > IV + V, AIII/E = 1.05, ascoids on IV = 0.4 length of segment. Palp: formula 1,(4,2),3,5, relative lengths 1, 3.8, 4.3, 3.6, 9. Epipharynx: length 0.35-0.4 mm. Pharynx: about twice as wide posteriorly as anteriorly, armed with small punctiform teeth arranged in transverse rows. Wing: length 3-3.4 mm., width 0.89-0.99 mm., alar index 1.85-2.64, delta + 0.19 to + 0.34 mm. Spermatheca: of major type, with 12-14 segments, a relatively long neck, and wide ducts opening separately into the vulva.

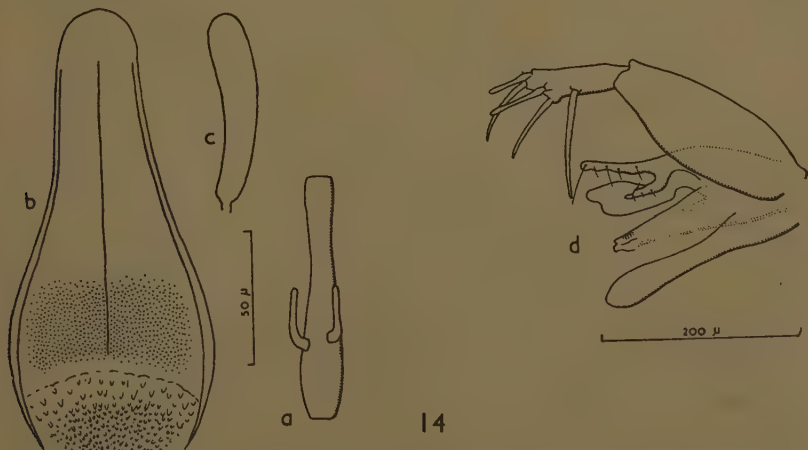
♂. Length: 2.7-2.8 mm., hind leg 4.8-5.7 mm. Antenna: formula 2/III-VII, 1/VIII-XV, segment III (0.45-0.52 mm.) > IV + V, AIII/E = 1.3-1.6, ascoids on IV = 0.3 length of segment. Palp: formula 1,(4,2),3,5, relative lengths 1, 3.3, 3.8, 3.1, 8. Epipharynx: length 0.3-0.34 mm. Pharynx: about twice as wide posteriorly as anteriorly and armed with transverse rows of fine punctiform teeth. Wing: length 2.56-3.0 mm., width 0.76-0.85 mm., alar index 2.1-2.7, delta + 0.23 to + 0.28 mm. Terminalia: coxite (0.37-0.44 mm.) less than twice length of style (0.21-0.24 mm.) which bears five long spines, two terminal and three submedian, of which two are borne on a process; paramere (0.23-0.27 mm.) expanded and cut away below at the distal end; penis sheath (0.14-0.16 mm.) with pointed distal end turned slightly upwards follows inferior border of paramere, but does not reach its distal end; lateral lobe (0.37-0.45 mm.) approximately as long as coxite.

Distribution: ABYSSINIA, A.-E. SUDAN.

Phlebotomus (Phlebotomus) lesleyae Lewis & Kirk.

P. lesleyae Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond.* (B) 15: 155.

Type Locality Kortala, Nuba Mountains A.-E. Sudan; type specimens in the British Museum. The description is based on examination of one male and one female.



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FIG. 14.—*P. lesleyae*, ♀: a, fourth antennal segment; b, pharynx; c, spermatheca. ♂: d, terminalia. (a, b and d after Lewis and Kirk, 1949; c from Kostis specimen.)

♀. *Length*: 1.9 mm. *Antenna*: formula 2/III-VIII (distal segments missing), segment III (0.15 mm.) < IV + V, AIII/E = 0.8, ascoids on IV = 0.2 length of segment. *Palp*: formula 1,2,3,..(4 and 5 missing), relative lengths 1, 2.7, 3.0..... *Epipharynx*: length 0.20 mm. *Pharynx*: twice as wide posteriorly as anteriorly, pigmented in middle, posterior third armed with strongly developed blunt teeth pointing inwards and backwards. *Wing*: length 1.48 mm., width 0.29 mm., alar index 0.3, delta -0.06 mm. *Spermatheca*: a thin-walled sac, without annulations.

♂. *Length*: 1.7 mm. *Antenna*: formula 2/III-XI (distal segments missing), segment III (0.12 mm.) < IV + V, AIII/E = 1.5, ascoids on IV = 0.2 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 1.8, 6.0, 4.0, 9.0. *Pharynx*: hardly wider posteriorly than anteriorly, unarmed except for faint ridges. *Wing*: length 1.14 mm., width 0.18 mm., delta -0.11 mm. *Terminalia*: coxite (0.21 mm.) twice as long as style (0.01 mm.), which bears five spines, one terminal, one subterminal, two at 0.7 and one very long spine at 0.3; paramere (0.19 mm.) consisting of an upper lobe bearing hairs and a lower lobe composed of a stem bearing a few hairs and of a thin, broad smooth plate; penis sheath (0.11 mm.) thick and conical with broad distal end, lightly pigmented; lateral lobe 0.2 mm.

With *P. heischii* and *P. gigas* this species presents the unusual feature in the subgenus *Phlebotomus* of having non-crenulated spermathecae. The male terminalia resemble those of certain Oriental species, *P. argentipes*, *P. philippinensis* etc., and on this character *P. lesleyae* has been incorporated with these by Theodor (1948) in the proposed subgenus *Euphlebotomus*.

Distribution: A.-E. SUDAN.

Phlebotomus (Phlebotomus) heischii Kirk & Lewis.

P. heischii Kirk & Lewis, 1950, *Proc. R. ent. Soc. Lond.* (B) 19: 11.

Type specimen in the British Museum. This species is known from one female specimen only from Wajir, Kenya.

♀ (damaged). *Antenna*: formula 2/III-XV, segment III (0.19 mm.) < IV + V, AIII/E = 0.8, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,4,2,3,5, relative

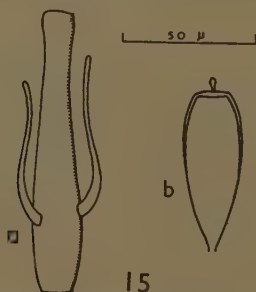


FIG. 15.—*P. heischii*, ♀: a, fourth antennal segment; b, spermatheca. (After Kirk and Lewis, 1950.)

lengths 1, 2.7, 4.0, 2.5, 6.3. *Epipharynx*: length 0.23 mm. *Pharynx* (lost): unarmed. *Wing*: length 1.5 mm., width 0.45 mm., alar index 0.9, delta +0.08 mm. *Spermatheca*: a sac without annulations.

♂. Unknown.

P. heischii is a member of the subgenus *Phlebotomus* with the unusual character of a non-segmented spermatheca, like that of *P. lesleyae* from which it differs by having long instead of very short ascoids.

Distribution: KENYA.

Phlebotomus (Phlebotomus) rodhaini Parrot.

P. rodhaini Parrot, 1930, *Rev. Zool. Bot. afr.* **19**: 181; *ibid.* **20**: 103.

P. rodhaini Parrot, 1948, *Arch. Inst. Pasteur Algér.* **26**: 121.

Type locality Mandimba (Lutubu), Belgian Congo; type specimen in the Museum of the Belgian Congo, Tervueren. The descriptions below are after Parrot, from four males and one female from the Congo and A.-E. Sudan.

♀. Length: 2 mm., hind leg 3.1 mm. Antenna: formula 2/III-XV, segment III (0.26 mm.) > IV + V, AIII/E = 1.1, ascoids on IV = 0.7 length of segment and project

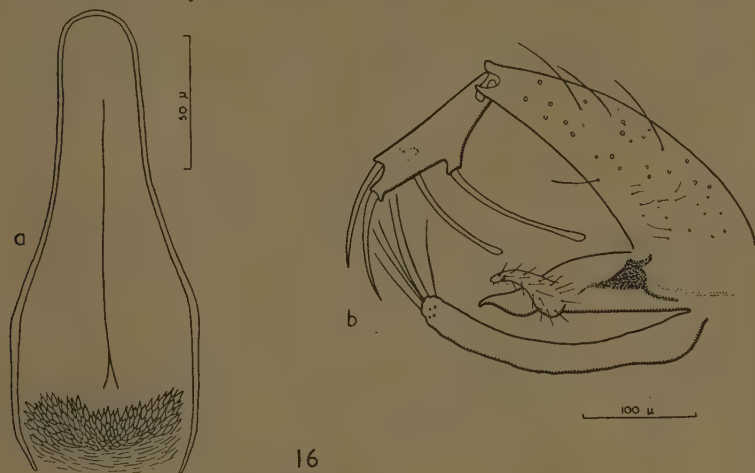


FIG. 16.—*P. rodhaini*, ♀: a, pharynx; ♂: b, terminalia. (After Parrot, 1948.)

beyond its tip. Palp: formula 1,4,2,3,5, relative lengths 1, 2.8, 4.1, 1.8, 5. Epipharynx: length 0.3 mm. Pharynx: about twice as wide posteriorly as anteriorly, constricted slightly in the middle of its wide part and bearing in its posterior third large scale-like spines which tend to become arranged in transverse lines posteriorly. Wing: length 1.78–2 mm., width 0.52–0.6 mm., alar index 1.7–1.8, delta + 0.15 mm. Spermatheca: annulated, details not made out (lost).

♂. Length: 1.7 mm., hind leg 2.65–2.8 mm. Antenna: formula 2/III-XIII, 1/XIV-XV, segment III (0.19–0.24 mm.) > IV + V, AIII/E = 1.4–1.7, ascoids on IV = 0.7 length of segment and project beyond it. Palp: formula 1,(4,2),3,5, relative lengths 1, 2.3, 4.3, 2.3, 6. Epipharynx: length 0.14–0.16 mm. Pharynx: slightly more than twice as wide posteriorly as anteriorly and bearing numerous transverse folds with fine punctiform teeth. Wing: length 1.47–1.58 mm., width 0.4–0.46 mm., alar index 1.6–2, delta + 0.034 mm. Terminalia: coxite (0.27–0.28 mm.) less than twice as long as style (0.14–0.15 mm.), which bears four spines, one terminal and external, one subterminal and internal, one at 0.75 internally and one at 0.5 externally; paramere (0.17–0.2 mm.) with two lobes,

an internal one bearing numerous hairs and an external one, chitimized, pigmented, with beak-like point and rounded ventral lobe; penis 0.05 mm., lateral lobe 0.26 mm.

Distribution: BELGIAN CONGO, A.-E. SUDAN.

Phlebotomus (Phlebotomus) gigas Parrot & Schwetz.

P. gigas Parrot & Schwetz, 1937, *Rev. Zool. Bot. afr.* 29: 224.

P. gigas Parrot & Wanson, 1938, *ibid.* 31: 153.

P. gigas Parrot & Wanson, 1946, *Arch. Inst. Pasteur Algér.* 24: 143.

Type locality Thysville, Belgian Congo; type specimens in the Museum of the Belgian Congo, Tervueren. A large, specialized, cave-dwelling form. The descriptions below are after Parrot and Wanson, from 74 males and 88 females.

♀. Length: 3.21-3.82 mm., hind leg 8.35-8.69 mm. Antenna: formula 2/III-XV, segment III (1-1.18 mm.) > IV + V, AIII/E = 2.3-2.5, ascoids slender and difficult to see, inserted at different levels in each segment, those of segment III being at 0.2 and 0.6, of segment IV at 0.3 and 0.6, the members of each pair being inserted nearer to each other towards the tip of the antenna, till in XIII, XIV and XV they are opposite each other.

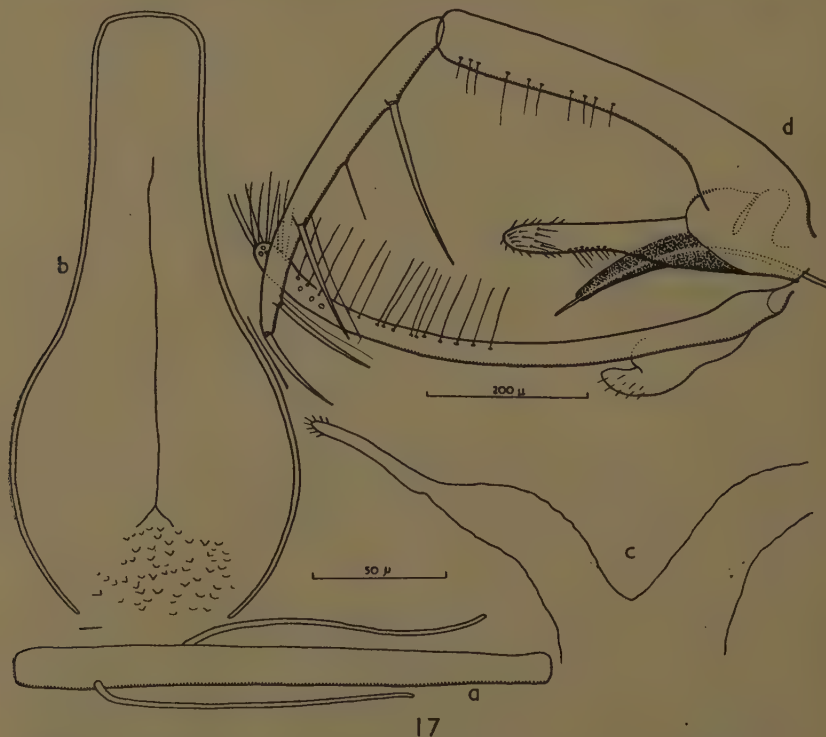


FIG. 17.—*P. gigas*, ♀: a, fourth antennal segment; b, pharynx; c, spermatheca. ♂: d, terminalia. (a-c after Parrot, 1948; d after Theodor, 1948.)

Palp: formula 1,4,2,5,3, relative lengths 1, 2.7, 4.5, 1.8, 2.8. *Epipharynx*: length 0.42–0.48 mm. *Pharynx*: about three times as wide posteriorly as anteriorly with some scale-like folds in its posterior part. *Wing*: length 3.7–3.75 mm., width 1.14–1.22 mm., alar index 4.7–5.3, delta + 0.75 to + 0.9 mm., pi – 0.24–0.32 mm. *Spermatheca*: non-segmented, opening into vulva by a short, very wide common duct, and having a long neck, bearing hairs and less chitinized than the rest of the organ.

♂. *Length*: 3.31–3.67 mm., hind leg 7.17–7.48 mm. *Antenna*: formula 2/III–IX (X), 1/X (XI)–XV, segment III (1.05–1.12 mm.) very long > IV + V, AIII/E = 4.4–4.9, ascoids long, slender, difficult to see and inserted at different positions in the different segments, those of III at 0.2 and 0.6, of IV at 0.3 and 0.6, while the insertions of those on the following segments become progressively closer to each other and to the base of the segment. *Palp*: formula 1,4,2,5,3, relative lengths 1, 2.6, 5.2, 2.2, 4.2. *Epipharynx*: length 0.21–0.24 mm. *Pharynx*: about 2.5 times as wide posteriorly as anteriorly and bearing some irregular tooth-like ridges. *Wing*: length 2.51–2.75 mm., width 0.8–0.9 mm., alar index 4–5.5, delta + 0.56 to + 0.65 mm., pi – 0.136 to – 0.17 mm. *Terminalia*: coxite (0.51–0.54 mm.) longer than style (0.42–0.49 mm.) which bears four long spines, one at 0.2, the second at 0.6, the third at 0.8 and the fourth terminal; non-deciduous seta inserted between first and second spines; paramere (0.36–0.38 mm.) finger-shaped, penis roughly conical but curved ventrally; lateral lobe (0.65–0.72 mm.) unarmed, longer than coxite.

Distribution: BELGIAN CONGO.

Phlebotomus (Sintonius) adleri Theodor.

P. adleri Theodor, 1933, *Bull. ent. Res.* 24: 537.

The description below is after Theodor's original description from six females and 11 males from Accra and Tamale, Gold Coast. Co-type ♂ and ♀ in the British Museum.

♀. *Length*: 1.9–2.45 mm. *Antenna*: segment III < IV + V, AIII/E = 0.65. *Palp*: formula, 1,2,4,3,5, relative lengths, 1, 1.8, 3.4, 2.4, 4.7. *Buccal cavity*: with a straight row of about 20 long pointed teeth; anteriorly 4–5 rows of small punctiform denticles; pigmented area large and roughly heart-shaped with a blunt forward apex. *Pharynx*: lamp-glass shaped, 2.5 times as wide posteriorly as anteriorly, with a few minute teeth.

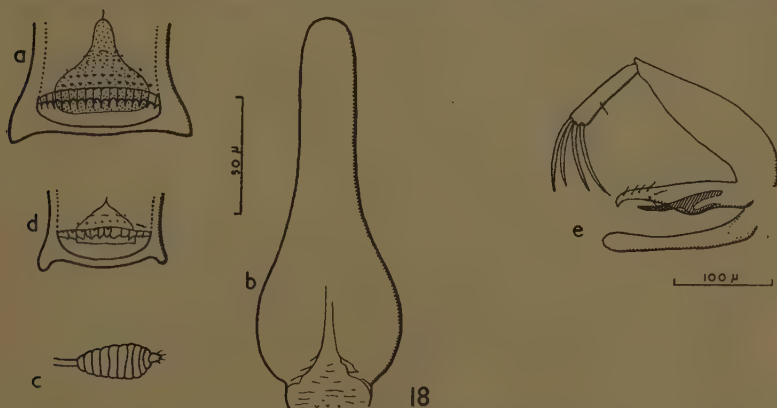


FIG. 18.—*P. adleri*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (After Theodor, 1933.)

Wing: 1.75–1.9 mm. long, 0.36–0.4 mm. wide, alar index 0.45. *Spermatheca*: with 10–12 segments and very long narrow ducts opening separately into the vulva.

♂. *Length*: 2 mm. *Antenna*: segment III < IV + V, AIII/E = 0.75–0.86. *Palp*: as in female. *Buccal cavity*: with 10–12 teeth in a straight line, in some specimens each tooth with 2–3 small secondary apical denticles; anteriorly 2–3 rows of small punctiform teeth; pigmented area faint, triangular with its apex forward. *Pharynx*: twice as wide posteriorly as anteriorly, lightly chitinized with some very faint ridges. *Wing*: 1.75 mm. long; 0.35 mm. broad, index 0.33–0.6. *Terminalia*: coxite twice, or slightly more, as long as style which bears four spines two terminal and two subterminal, and small non-deciduous seta at 0.5; paramere moderately beaked; penis sheath pointed, tapering and bent slightly upwards; lateral lobe shorter than coxite.

Distribution: GOLD COAST, A.-E. SUDAN.

Phlebotomus (Sintonius) affinis Theodor.

P. affinis Theodor, 1933, *Bull. ent. Res.* 24: 537.

P. affinis Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26: 122.

The description below is after Theodor and Parrot's descriptions of two females from the type locality (southern A.-E. Sudan, probably near Kapoeta) and Li Rangu, and from the examination of additional females and 2 males from the Sudan.

♀. *Length*: 2.2–2.3 mm. *Antenna*: segment III (0.20 mm.) > IV + V, AIII/E = 1.1–1.15, formula 2/III–XV, ascoids on IV = 0.33 length of segment. *Palp*: formula 1, 2, 3, 4, 5, relative lengths, 1, 2.4, 3, 4, 7.5. *Epipharynx*: length 0.18 mm. *Buccal cavity*: with a slightly or strongly retroconvex row of 34–40 monomorphic, narrow, parallel teeth with short points; pigmented area a narrow elongated ellipse, reaching or nearly reaching the sides of the buccal cavity, with a pale subtriangular forward process; well marked

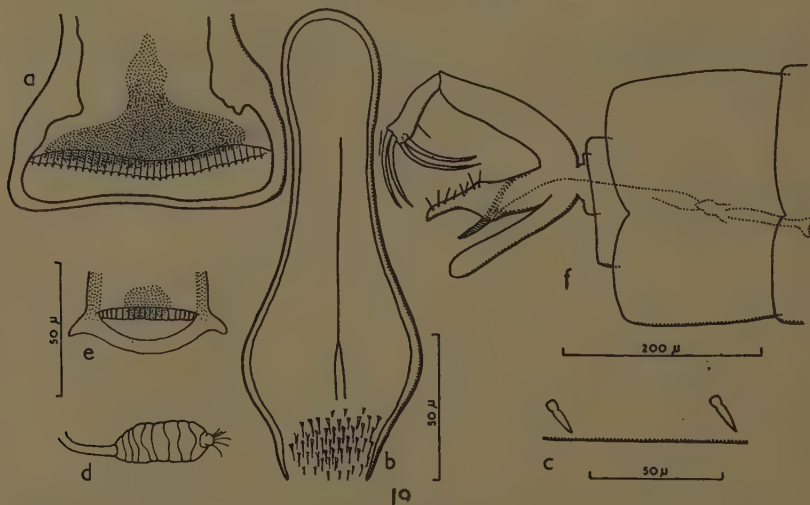


FIG. 19.—*P. affinis*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spines on hind femur; *d*, spermatheca. ♂: *e*, buccal cavity; *f*, terminalia (*a*, *b* and *d* after Parrot, 1948; *c* and *f* from Mvolo specimen).

anterior buccal protuberances with irregular medial margins. *Pharynx*: lamp-glass shaped, 2.5–3 times as wide posteriorly as anteriorly, with relatively few (about 50) strong teeth with long points. *Wing*: 1.94 mm. long, 0.45 mm. broad, alar index 0.9, delta + 0.221 mm. *Legs*: femora (anterior and posterior) armed with up to 10 spines. *Spermatheca*: with 8–9 segments and long narrow ducts.

♂. *Length*: 3.0 mm. *Antenna*: formula 1/III–XV, ascoid on IV = 0.2 length of segment, segment III (0.22 mm.) > IV + V, AIII/E = 1.3. *Palp*: formula 1,2,3,4,5, relative lengths, 1, 2.2, 3.4, 4, 7.5. *Buccal cavity*: with a straight row of about 16 blunt teeth of which the middle ones are parallel to each other and the outer ones incline towards the centre; pigmented area rounded anteriorly except for a small pale forward process. *Pharynx*: lamp-glass shaped, 1.5 times as wide posteriorly as anteriorly, with a few transverse ridges and minute spicules. *Wing*: 1.77 mm. long, 0.42 mm. broad, alar index 0.69 delta + 0.10 mm. *Terminalia*: coxite twice as long as style, which bears four terminal spines and small non-deciduous seta at 0.5; paramere beaked; penis sheath small, slender, and tapering to a sharp point.

Distribution: A.-E. SUDAN.

Phlebotomus (Sintonius) affinis var. *vorax* Parrot.

P. affinis Lewis & Kirk, 1940, *Proc. R. ent. Soc. Lond. (B)* 9: 127.

P. affinis var. *vorax* Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26: 121.

The descriptions below are from the original descriptions, partly after Parrot, of one female and one male from the type locality El Fasher, A.-E. Sudan. Type specimens in the British Museum (Natural History).

♀. *Length*: 2.16 mm. *Antenna*: missing. *Palp*: formula, 1,2,3,4,5, relative lengths, 1, 3.5, 4.5, 5.5, 7.5. *Epipharynx*: length 0.17 mm. *Buccal cavity*: with 56 monomorphic narrow teeth with long points in a palisade slightly convex posteriorly; pigmented area

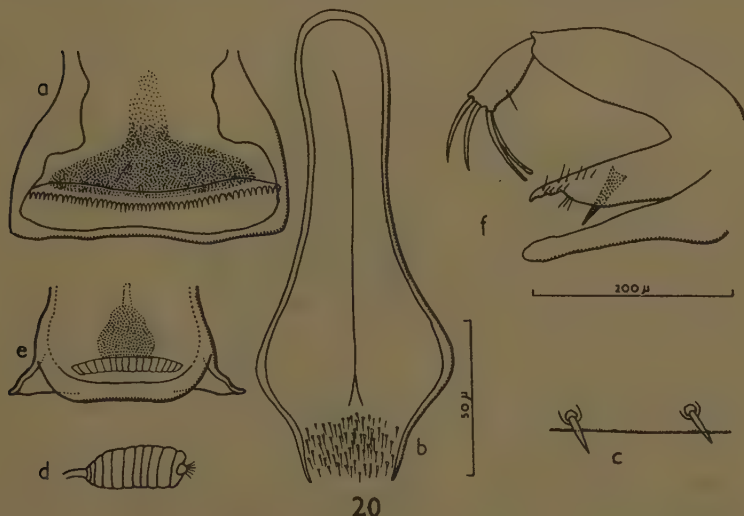


FIG. 20.—*P. affinis* var. *vorax*, ♀: a, buccal cavity; b, pharynx; c, spines on hind femur; d, spermatheca. ♂: e, buccal cavity; f, terminalia. (a–d and f after Parrot, 1948; e after Lewis and Kirk, 1940.)

an elongated ellipse with pale triangular forward extension; anteriorly lateral buccal protuberances are well marked, with irregular inner edges. *Pharynx*: lamp-glass shaped, 2.5 times as wide posteriorly as anteriorly, armed with over 60 spines with long points. *Wing*: missing. *Legs*: the one existing femur bearing 10 short and strong femoral spines. *Spermatheca*: with 10-11 segments and a narrow duct.

♂. *Length*: 3.09 mm. *Antenna*: formula I/III-XV, segment III (0.21 mm.) > IV + V, AIII/E = 1.2; ascoid on IV = 0.2 length of segment. *Palp*: formula, 1,2,3,4,5, relative lengths, 1, 3.4, 4.9, 5.5, 9.5. *Epipharynx*: length 0.17 mm. *Buccal cavity*: with 15 broad teeth arranged in a straight line; pigmented area half moon shaped, with ragged posterior border. *Pharynx*: lamp-glass shaped, less than twice as wide posteriorly as anteriorly, with a few transverse ridges bearing small denticles in its posterior part. *Wing*: 1.78 mm. long, 0.42 mm. broad, alar index 0.68, delta + 0.051 mm. *Terminalia*: coxite (0.21 mm.) more than twice as long as style (0.084 mm.) which bears four terminal spines and small non-deciduous seta at 0.6; paramere (0.18 mm.) slightly beaked; penis sheath (0.066 mm.) elongated, conical, with blunt point; lateral lobe, 0.20 mm.

Distribution: A.-E. SUDAN.

Phlebotomus (Sintonius) caffrarius De Meillon & Lavoipierre.

P. caffrarius De Meillon & Lavoipierre, 1944, *J. ent. Soc. S. Afr.* 8: 38.

Type locality Bizana, Transkei, Cape Province; type specimen in South African Institute for Medical Research. This species is known from one female only the description of which is after De Meillon and Lavoipierre.

♀. *Length*: 3.56 mm. *Antenna*: formula 2/III-XV, ascoids on IV = 0.5 length of segment, segment III (0.26 mm.) < IV + V, AIII/E = 0.86. *Palp*: formula, 1,2,4,3,5,

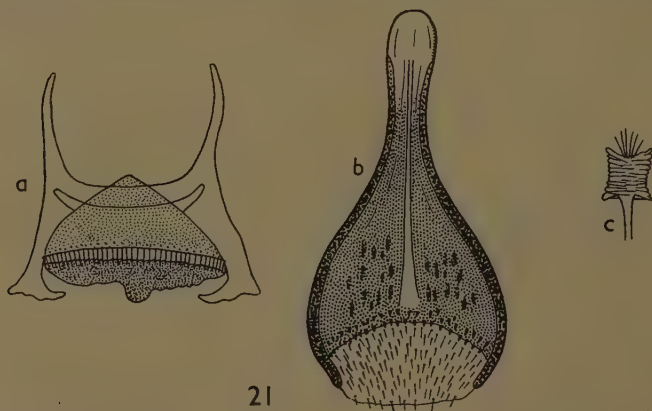


FIG. 21.—*P. caffrarius*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. (After De Meillon and Lavoipierre, 1944.)

relative lengths 1, 1.7, 2.7, 2.3, 4.3. *Epipharynx*: length 0.3 mm. *Buccal cavity*: with about 40 nearly equal, pointed teeth in an even row, anteriorly a row of fine punctiform denticles, pigmented area almost black with ragged posterior edge and prominent posterior median lobe. *Pharynx*: nearly 4.5 times as wide posteriorly as anteriorly, densely pigmented except for posterior part, which bears numerous fine teeth with two irregular rows of strong short spines along the posterior margin of the dorsal plate (other spines, anterior to these,

shown in the figure). *Wing*: length 2.4 mm. breadth 0.7 mm., alar index 1.1, delta : + 0.24 mm. *Spermatheca*: 0.024 mm. long and 0.02 mm. wide, finely striated transversely, but not distinctly segmented (figured from specimen expanded in hot lacto-phenol).

♂. Unknown.

Distribution: CAPE PROVINCE.

Phlebotomus (Sintonius) christophersi Sinton.

P. christophersi Sinton, 1927, *Indian J. med. Res.* 15 : 33.

P. christophersi Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26 : 121.

Dr. L. Parrot has examined specimens from the A.-E. Sudan and considers that the examination of further, well-preserved, specimens will confirm the existence of the Indian *P. christophersi* in Africa. The above-mentioned specimens, which came from a remote area are provisionally regarded as *P.*

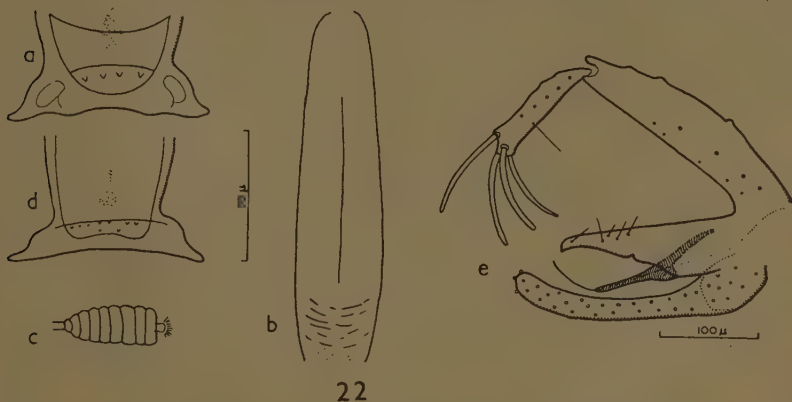


FIG. 22.—*P. christophersi*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. (*a* and *c-e* after Sinton, 1927; *b* from Mvolo specimen.)

christophersi and the description of this species given below has been compiled from Sinton's original description of seven females and five males from the Punjab, and one female (buccal teeth) from the Punjab, examined by Dr. Parrot.

♀. *Length*: 2.5–2.83 mm. *Colour*: the very dark eyes are in contrast to the lighter sides of the thorax. *Antenna*: formula 2/III–XV, ascoids stout and well developed, those on IV = 0.5 length of segment; segment III (0.114–0.143 mm.) < IV + V. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.6, 4.9, 3.2, 7.5. *Buccal cavity*: with four or five widely separated and well developed teeth and two groups of lateral denticles in at least one specimen; pigmented area small, carrot-shaped. *Wing*: 1.57–1.73 mm. long, 0.37–0.43 mm. broad, alar index 0.51–0.75, delta + 0.057 to + 0.085 mm. *Spermatheca*: with 8–9 segments.

♂. *Length*: 2.4–2.7 mm. *Antenna*: formula 1/III–XV, ascoids well developed, that on IV = 0.3 length of segment, segment III (0.14–0.157 mm.) < IV + V. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.8, 5, 3.7, 8.7. *Buccal cavity*: with two or three large teeth and some smaller ones anterior to them; pigmented area carrot-shaped. *Wing*: 1.50–1.63 mm. long, 0.357–0.370 mm. broad, alar index 0.15–0.64, delta – 0.114 to +

0.028 mm. *Terminalia*: coxite (0.23–0.255 mm.), style (0.11–0.12 mm.) with four terminal spines and small ventral seta at 0.75; paramere (0.165–0.218 mm.) hooked and having a very distinct narrow fissure on its concave margin about one-third of its length from the apex; penis sheath (0.055–0.057 mm.) sharply pointed; lateral lobe 0.165–0.225 mm.

Variation: Dr. Parrot has pointed out that the males from the Sudan have strongly developed buccal teeth and resemble *P. christophersi* var. *calcaratus*, except in the absence of femoral spines.

Distribution: A.-E. SUDAN (Mvolo).

Phlebotomus (Sintonius) christophersi var. *calcaratus* Parrot.

P. calcaratus Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26: 121.

This sandfly has been provisionally placed as a variety following a suggestion from Dr. Parrot. Type specimens in the British Museum (Natural History). The descriptions given below are after Parrot's original description of two females and one male from, Agordat, Kassala, and Jebel Moya.

♀. Length: 2.18–2.19 mm. Antenna: formula 2/III–XV, segment III (0.15 mm.) < IV + V, AIII/E = 0.9, ascoids on IV = 0.35 length of segment. Palp: formula

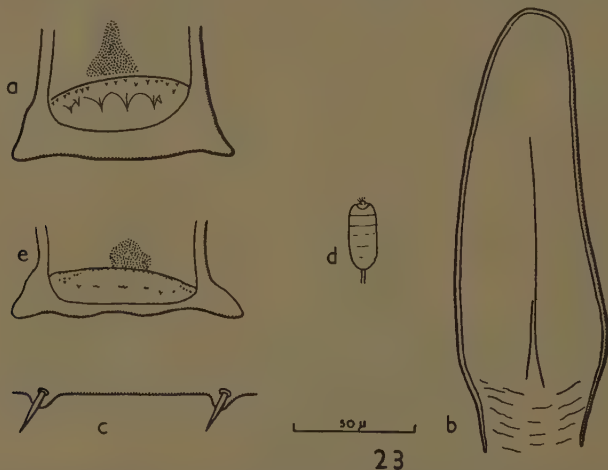


FIG. 23.—*P. christophersi* var. *calcaratus*, ♀: a, buccal cavity; b, pharynx; c, spines on femur; d, spermatheca. ♂: e, buccal cavity. (a–c and e after Parrot, 1948; d from Rashad specimen.)

1,2,4,3,5, relative lengths 1, 2, 4.9, 4.4, 9.5. *Epipharynx*: length 0.15 mm. *Buccal cavity*: with four widely separated pointed teeth, better developed than in *P. christophersi*, standing on a straight line, the two median ones a little stronger than the laterals (in one specimen two additional smaller teeth present, out of line with the others), anteriorly 12–16 pointed or punctiform denticles (more than in *P. christophersi*), irregularly arranged; pigmented area an elongated triangle truncated anteriorly. *Pharynx*: less than twice as wide posteriorly as anteriorly, with some sinuous folds. *Wing*: 1.62 mm. long, 0.36 mm. broad, alar index 0.36–0.41, delta – 0.017 mm., pi = 0 to – 0.034 mm.

Legs : four short spines on the anterior and posterior femora. *Spermatheca* : annulated with segments.

♂. *Length* : 2.16 mm. *Antenna* : formula 1/III-XV, segment III (0.135 mm.) < IV + V, AIII/E = 0.75, ascoid on IV = 0.33 length of segment. *Palp* : formula 1,2,4,3,5, relative lengths 1, 2.3, 4.6, 4.1, 7.7. *Epipharynx* : length 0.18 mm. *Buccal cavity* : with five widely separated teeth nearly in a straight line, the lateral ones short and pointed, the three inner ones wider and each composed of several denticles ; anteriorly many punctiform denticles in groups of 3 or 4 or more, other punctiform or pointed denticles at the sides ; pigmented area subtriangular and equilateral. *Pharynx* : a little less than twice as wide posteriorly as anteriorly, with numerous short, but well-marked spines. *Wing* : 1.5 mm. long, 0.34 mm. broad, alar index 0.56, delta + 0.017 mm. *Legs* : 4-5 short spines on anterior and 10 on posterior femora. *Terminalia* : coxite (0.255 mm.) a little less than twice as long as style (0.138 mm.) which bears two terminal and two subterminal spines and small ventral seta at 0.75 ; paramere (0.164 mm.) shorter than lateral lobe, hooked ; penis sheath (0.114 mm.) an elongated cone slightly turned up towards the point, which is blunt ; lateral lobe (0.225 mm.) unarmed.

Distribution : A.-E. SUDAN.

Phlebotomus (Sintonius) clydei Sinton.

P. clydei Sinton, 1928, *Indian J. med. Res.* 16 : 179.

P. vagus Parrot & Martin, 1939, *Arch. Inst. Pasteur Algér.* 17 : 143.

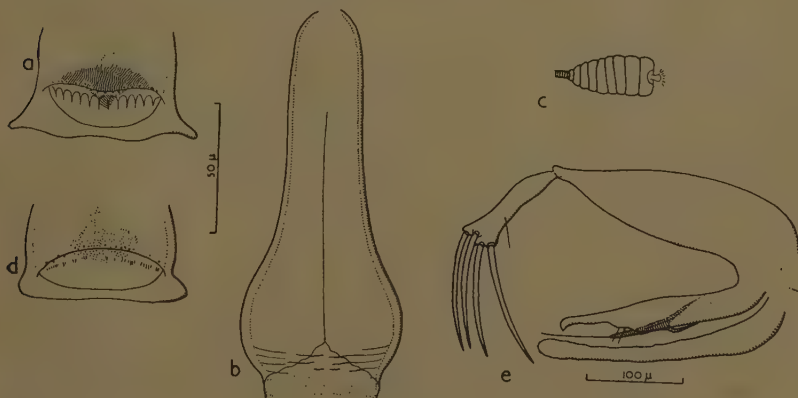
P. viator Parrot & Martin, 1939, *ibid.* 17 : 143.

P. clydei Lewis & Kirk, 1939, *Proc. R. ent. Soc. Lond. (B)* 8 : 155.

P. clydei Parrot & Martin, 1944, *Arch. Inst. Pasteur Algér.* 22 : 55.

P. clydei Parrot, Mornet & Cadenat, 1945, *ibid.* 23 : 232.

The descriptions given below are from the original descriptions of 11 females and 10 males from Waziristan, India, and from published descriptions of about 63 females and 45 males, certain measurements from smaller numbers. Type specimen is in the British Museum.



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FIG. 24.—*P. clydei*, ♀: *a*, buccal cavity ; *b*, pharynx ; *c*, spermatheca. ♂: *d*, buccal cavity ; *e*, terminalia. (*a* and *b* from Wad Medani specimens ; *c* and *a* after Parrot and Martin, 1939 ; *d* after Parrot and Martin, 1944.)

♀. *Length*: 1.88–2.63 mm. *Antenna*: formula 2/III–XV, segment III (0.138–0.165 mm.) < IV + V, AIII/E = 0.62–0.75, ascoids on IV slightly less than 0.5 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.4, 3.8, 2.9, 6.2. *Epipharynx*: length 0.214–0.228 mm. *Buccal cavity*: with 12–16 strong pointed teeth, the two median ones sometimes smaller than the others; about 18 anterior denticles in one or two rows, the anterior of which contains smaller and fewer denticles, sometimes very few; pigmented area pale brown, shaped like an irregular lozenge with its axis transverse and its lateral and posterior extremities rounded, with a pale forward prolongation. *Pharynx*: a little more than twice as wide posteriorly as anteriorly with a delicate armature, which is often difficult to see, composed of transverse ridges, the posterior of which bear minute spicules. *Wing*: 1.58–1.88 mm. long, 0.45–0.46 mm. broad, alar index 0.61–0.97, delta + 0.035 to + 0.085 mm. *Spermatheca*: with 8–10 segments, narrower towards the duct.

♂. *Length*: 1.9–2.8 mm. *Antenna*: formula 1/III–XV, segment III (0.153–0.185 mm.) < IV + V, AIII/E = 0.83–0.85, ascoid on IV = 0.4 length of segment. *Palp*: formula, 1,2,4,3,5, relative lengths 1, 2.8, 4.7, 3.6, 8.2. *Buccal cavity*: with small pointed teeth, usually in groups of 4–6, on an arc slightly concave posteriorly, anteriorly a row of six or more rather strong rounded denticles; pigmented area a pale brown slightly elongated ellipse. *Pharynx*: about 2.5 times as wide posteriorly as anteriorly, with a faint armature or none. *Wing*: 1.54–1.82 mm. long, 0.36–0.44 mm. broad, alar index 0.55–0.97, delta + 0.028 to + 0.114 mm. *Terminalia*: coxite (0.213–0.271 mm.) more than twice as long as style (0.10–0.12 mm.), which bears two terminal and two subterminal spines and small ventral seta at about 0.7; paramere (0.168–0.225 mm.) hooked, shorter than lateral lobe; penis sheath (0.045–0.072 mm.) a bluntly pointed elongated cone with the tip slightly turned up; lateral lobe 0.270 mm.

Distribution: A-E. SUDAN, ABYSSINIA, DJIBUTI, SENEGAL, FRENCH NIGER, FRENCH SUDAN, ERITREA; also in MEDITERRANEAN BASIN, INDIA AND MIDDLE ASIA.

Phlebotomus (Sintonius) meilloni Sinton.

P. meilloni Sinton, 1932, *Indian J. med. Res.* 20 : 565.

The description given below is after the original description of 4 females and seven males from the type locality Letsitelle (measurements from 4 females and 4 males). Type specimens are in the British Museum.

♀. *Length*: 2.81–3.1 mm. *Antenna*: formula 2/III–XV, segment III very long (0.29–0.31 mm.) > IV + V, ascoids short, that on IV = 0.25 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.6, 3.7, 4.6, 7.1. *Buccal cavity*: with about 16 large pointed teeth standing almost in a straight line; a well marked mushroom-shaped pigmented area. *Pharynx*: about twice as wide posteriorly as anteriorly, with groups of minute spines along small ridges, the posterior spines longer than the anterior ones. *Wing*: 2.143–2.300 mm. long, 0.643–0.685 mm. broad, alar index 1.66, delta + 0.357 to + 0.385 mm. *Spermatheca*: with eight segments.

♂. *Length*: 2.64–3.4 mm. *Antenna*: formula 1/III–XV, segment III very long (0.36–0.40 mm.) = IV + V. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.8, 3.9, 4.8, 8.5. *Buccal cavity*: about 10 teeth, wider than in the female and often serrated, pigmented area small but distinct, turnip-shaped. *Pharynx*: less dilated posteriorly and more lightly armed than in the female. *Wing*: 2.0–2.4 mm. long, 0.52–0.66 mm. broad, alar index 1.26–1.66, delta + 0.285 to + 0.38 mm. *Terminalia*: coxite (0.27–0.32 mm.) about 2.2 times as long as style, which bears four curved spatulate spines, two terminal and two subterminal and small ventral seta near the subterminal spines; paramere 0.21–0.255 mm.; penis sheath 0.174–0.210 mm., pointed; lateral lobe 0.24–0.28 mm.

Distribution: TRANSVAAL, SOUTH AFRICA (LETSITELLE).

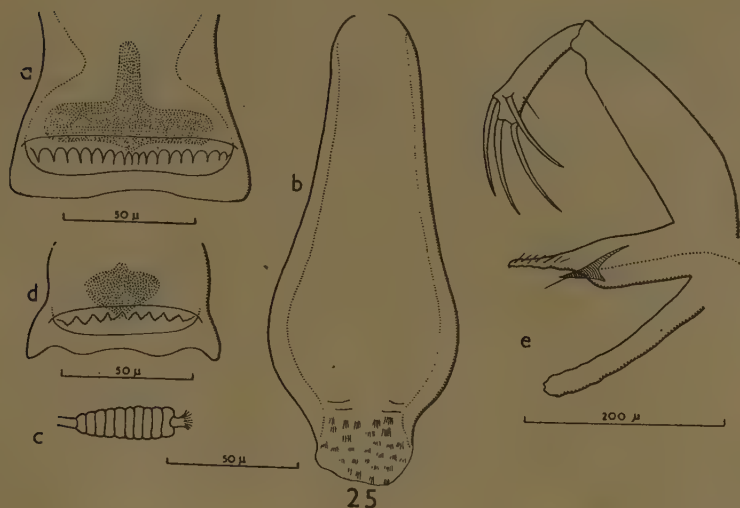


FIG. 25.—*P. meilloni*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. (After Sinton, 1932.)

Phlebotomus (Sintonius) meilloni var. *suberectus* Sinton.

P. meilloni var. *suberectus* Sinton, 1932, *Indian J. med. Res.* 20: 565.

Type locality Mombasa, Kenya, type specimens in the British Museum. This form may prove to be a species when the female is described. The description below is from two males, after Sinton.

♀. Unknown.

♂. Length: 3.2 mm. Antenna: formula 1/III-XV, segment III (0.34–0.36 mm.) > IV + V, ascoids relatively longer than in *P. meilloni*, that on IV = 0.2 length of segment. Palp: formula 1,2,3,4,5, relative lengths 1, 2.3, 3.6, 4.9, 8.8. Buccal cavity: with about 22–25 teeth, much smaller than in *P. meilloni*, on an arc concave posteriorly. Pharynx: more dilated than in *P. meilloni* posteriorly. Wing: 2.26 mm. long and 0.67–0.68 mm. broad, relatively wider than in *P. meilloni*, alar index 1.86–2.1, delta + 0.400 to + 0.443 mm. Terminalia: coxite (0.30–0.32 mm.) more than twice as long as style (0.14–0.15 mm.), which bears small ventral seta distinctly proximal to the large spines and the two subterminal of these more proximal than in *P. meilloni*; paramere 0.246 mm., penis sheath 0.185–0.2 mm., lateral lobe 0.29–0.30 mm.

Distribution: KENYA (MOMBASA).

Phlebotomus (Sintonius) subtilis Parrot and Martin.

P. tiberiadis Parrot, 1936, *Arch. Inst. Pasteur Algér.* 15: 44.

P. subtilis Parrot & Martin, 1939, *ibid.* 17: 143.

P. subtilis Parrot & Martin, 1940, *ibid.* 18: 300.

P. subtilis Parrot, 1948, *ibid.* 26: 259.

Type locality Awash, Abyssinia; type specimens in the Institut Pasteur d'Algérie. The descriptions given below are after Parrot (1948) from the

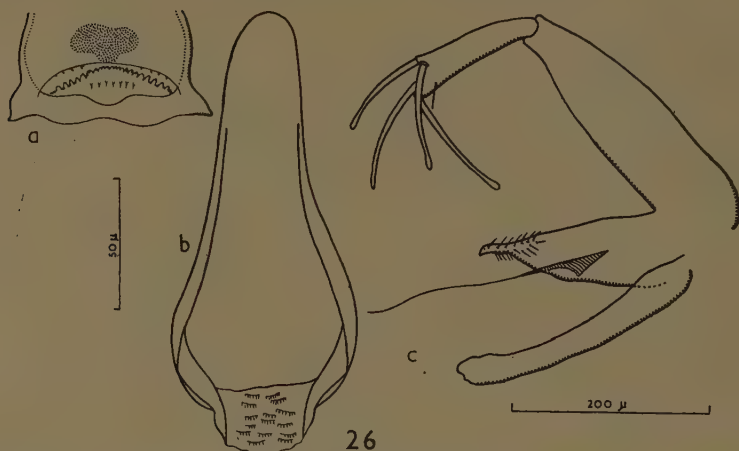


FIG. 26.—*P. meillonii* var. *suberectus*, ♂: *a*, buccal cavity; *b*, pharynx; *c*, terminalia. (After Sinton, 1932.)

published descriptions of 128 females and 463 males from Abyssinia, French Somaliland and the A.-E. Sudan.

♀. *Length*: 1.5–1.9 mm. *Antenna*: formula 2/III–XV, segment III (0.14–0.18 mm) < IV + V, AIII/E = 0.6–0.75, ascoids on IV = 0.4 length of segment. *Palp*: formula 1, 2, 4, 3, 5, relative lengths 1, 2.2, 4.5, 3, 7. *Epipharynx*: length 0.21 mm. *Buccal cavity*: with 18 broad pointed teeth arranged almost in a straight line, the lateral teeth being broader than the median ones and pointing obliquely posteriorly and medially; two rows of anterior punctiform teeth, the first of 14–16 being more prominent than the second, which has 10–12 teeth; pigmented area in the form of an ellipse lying transversely with

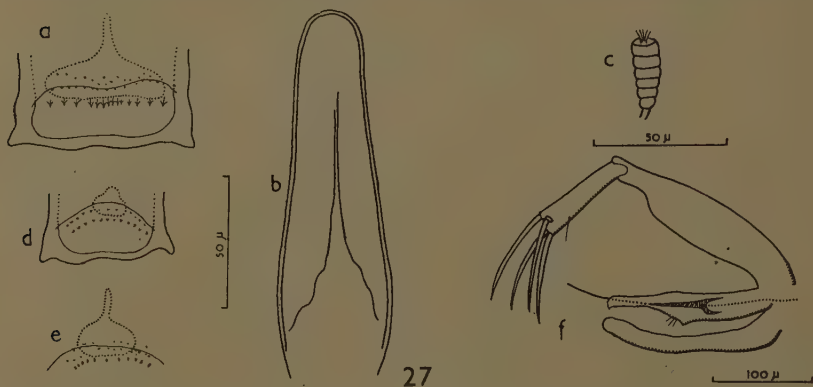


FIG. 27.—*P. subtilis*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d* and *e*, buccal cavity in Gallabat and Massawa specimens; *f*, terminalia. (*a*, *d* and *e* after Parrot, 1948; *b* and *c* after Parrot, 1936; *f* after Parrot and Martin, 1939.)

an anterior prolongation. *Pharynx*: 1.5 times as wide posteriorly as anteriorly. *Wing*: 1.4–1.7 mm. long, 0.33–0.43 mm. broad, alar index 0.5–0.8, delta 0 to + 0.7 mm. *Spermatheca*: with 6–8 segments, decreasing in width towards the duct, which is narrow and opens separately into the vulva.

♂. *Length*: 1.4–1.8 mm. *Antenna*: formula 1/III–XV, segment III (0.12–0.16 mm.) < IV + V, AIII/E = 0.8–0.9, ascoid on IV = 0.4 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths of segments 1, 2.5, 4.9, 3.7, 7.5. *Epipharynx*: length 0.15–0.19 mm. *Buccal cavity*: with 12–14 pointed teeth, the points directed obliquely towards the centre, and the median teeth smaller than the lateral ones; anteriorly a row of 6 median punctiform denticles with 6–8 larger denticles on each side; pigmented area small, faint, centrally situated. *Pharynx*: less than twice as wide posteriorly as anteriorly, armed with a few fine ridges. *Wing*: 1.2–1.4 mm. long, 0.24–0.30 mm. broad, alar index 0.35–0.57, delta – 0.2 to + 0.3 mm. *Terminalia*: coxite (0.16–0.2 mm.) more than twice as long as style, which bears four terminal spines and small non-deciduous seta at 0.75; paramere (0.136–0.165 mm.) hooked, as long as lateral lobe; penis sheath (0.06 mm.) an elongated and slender cone with blunt tip.

Distribution: ABYSSINIA, ERITREA, A.-E. SUDAN.

Phlebotomus (Sintonius) thomsoni Theodor.

P. thomsoni Theodor, 1938, *Bull. ent. Res.* 24: 165.

The descriptions below are after the original descriptions of 3 females and one male from Port Johnson, Nyasaland, the type locality.

♀. *Length*: 2.7 mm. *Antenna*: segment III > IV + V, AIII/E = 1.7. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.2, 5, 6, 9.5. *Buccal cavity*: with a nearly straight

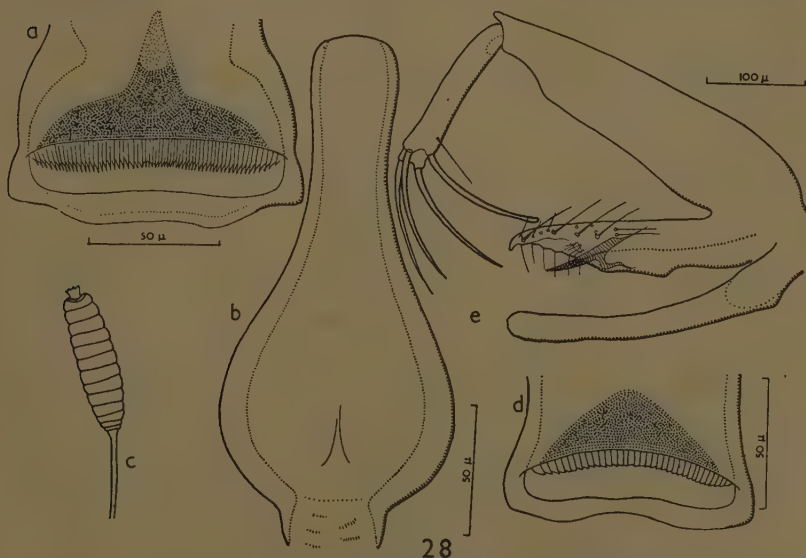


FIG. 28.—*P. thomsoni*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. (After Theodor, 1938.)

row of 55-60 narrow parallel teeth with long points, the median teeth slightly narrower than the lateral ones, pigmented area rounded anteriorly and straight posteriorly with a long triangular forward process. *Pharynx*: lamp-glass shaped, with very thick walls, three times as wide posteriorly as anteriorly, with some rows of very small teeth. *Wing*: 2.4 mm. long, 0.65 mm. broad, alar index 1.7. *Spermatheca*: with 10-12 segments and a short terminal process.

♂. *Length*: 2.8 mm. *Antenna*: segment III = IV + V, AIII/E = 1.8. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.6, 5.3, 6.3, 9.5. *Buccal cavity*: with a slightly curved row of 35 short parallel teeth with blunt points; pigmented area broad and triangular. *Terminalia*: coxite more than twice as long as style, two of the four spines markedly subterminal and the small ventral seta arising near the subterminal spines; paramere hooked, with some long hairs; penis sheath straight and tapering to a sharp point.

Distribution: NYASALAND, A.-E. SUDAN.

Phlebotomus (Sintonius) transvaalensis Sinton.

P. transvaalensis Sinton, 1933, *Indian J. med. Res.* 20 : 879.

Type locality Tzaneen, Transvaal. This species is known by one female only, the description of which given below is after Sinton.

♀. *Length*: 3.75 mm. *Colour*: a very dark insect with dorsal abdominal tufts of erect golden yellow hairs. *Antenna*: formula 2/III-XV, ascoids slender, segment III

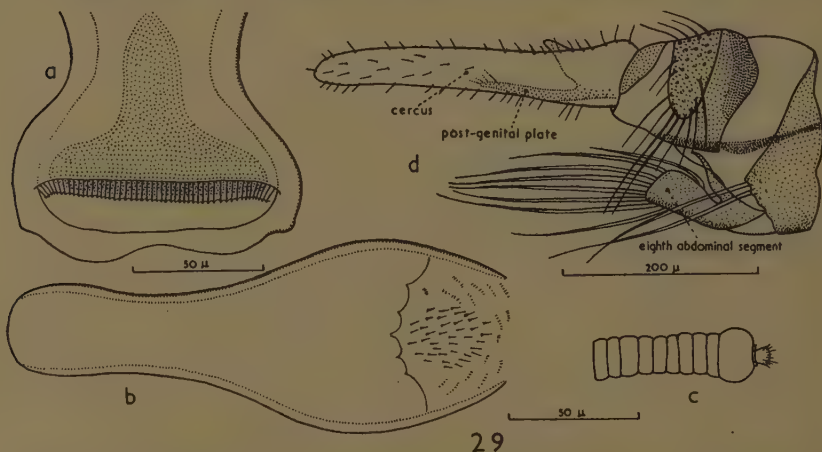


FIG. 29.—*P. transvaalensis*, ♀: a, buccal cavity; b, pharynx; c, spermatheca; d, terminalia. (After Sinton, 1933.)

(0.315 mm.) > IV + V. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.7, 3.1, 3.3, 7.5. *Buccal cavity*: with a nearly straight row of about 50 narrow teeth; pigmented area well developed. *Pharynx*: not very wide posteriorly, with some small median teeth and lateral rows of very minute teeth. *Wing*: 2.57 mm. long, 0.343 mm. broad. *Spermatheca*: with 10 segments. *Terminalia*: cerci very long and narrow; eighth sternite with some very stout long bristles on its posterior border; post genital plate a very elongated triangle, not rectangular as in other species.

This species is readily distinguished from all the other species by the characters of the female terminalia.

♂. Unknown.

Distribution : TRANSVAAL.

Phlebotomus (Sintonius) wansoni Parrot.

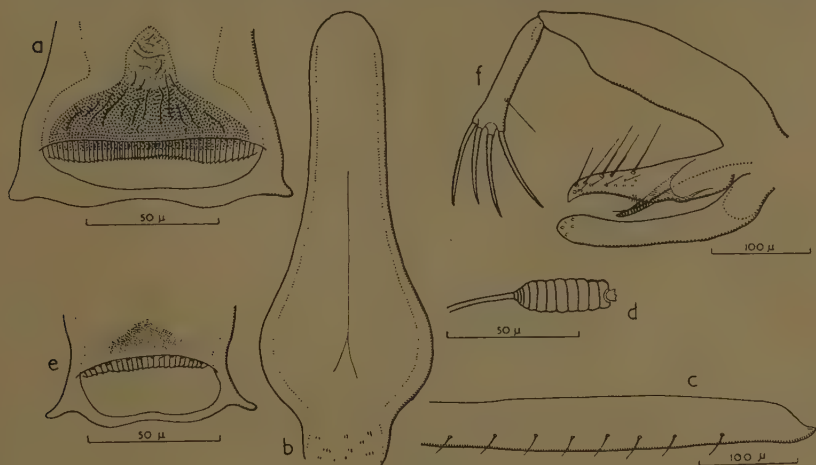
P. wansoni Parrot, 1938, *Rev. Zool. Bot. afr.* **30** : 361.

P. matadiensis Theodor, 1938, *Bull. ent. Res.* **29** : 165.

P. wansoni Parrot, 1939, *Rev. Zool. Bot. afr.* **32** : 145.

Type specimens in the Museum of the Belgian Congo, Tervueren. The descriptions below are after Parrot's and Theodor's descriptions 4 males and four females, all from Matadi, Belgian Congo.

♀. Length : 1.7-2.4 mm. Antenna : formula 2/III-XV, segment III (0.21 mm.) > IV + V AIII/E = 1.14-1.17, ascoids on IV = 0.3 length of segment. Palp : formula 1,2,3,4,5. Buccal cavity : with a row, straight or slightly convex posteriorly, of 50-60



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FIG. 30.—*P. wansoni*, ♀: a, buccal cavity; b, pharynx; c, spines on femur; d, spermatheca. ♂: e, buccal cavity; f, terminalia. (a, b and d-f after Theodor, 1938; c after Parrot, 1938.)

monomorphic parallel teeth with short points, the median teeth slightly narrower than the lateral ones; pigmented area dark brown, with corrugated lines converging anteriorly, reaching the sides of the buccal cavity and having a paler truncated forward process. Pharynx : lamp-glass shaped, 2.5 times as wide posteriorly as anteriorly, with some very minute teeth or none visible. Wing : 1.6-2 mm. long, 0.46-0.6 mm. broad, alar index 1.05-1.47, delta + 0.19 to + 0.21 mm. Legs : fore and hind femora with short spines on the posterior surface of the proximal half, five spines on the anterior and seven on the posterior. Spermatheca : with 10-12 segments.

♂. Length : 2-2.15 mm. Antenna : formula 1/III-XV, ascoids short, segment III (0.26 mm.) > IV + V, AIII/E = 1.36-1.45. Palp : formula 1,2,3,4,5, relative lengths 1, 4, 6, 7, 11. Epipharynx : length 0.18-0.19 mm. Buccal cavity : with a row, slightly

concave posteriorly, of 18-25 narrow, parallel teeth, the lateral teeth slightly narrower and shorter than the median ones; pigmented area dark brown and subtriangular. *Pharynx*: like that of the female but narrower, a little less than twice as wide posteriorly as anteriorly. *Wing*: length 1.82-1.86 mm., breadth 0.47-0.51 mm., alar index 1.23 to 1.37, delta + 0.23 mm. *Terminalia*: coxite (0.22-0.23 mm.) about twice as long as style (0.10-0.11 mm.), which bears four terminal spines and small ventral seta at 0.7; paramere 0.18-0.19 mm., long hooked and tapering at the tip; penis sheath tapering to a sharp point and slightly curved upwards; lateral lobe (0.2-0.21 mm.) a little shorter than paramere.

Distribution: BELGIAN CONGO. UGANDA.

Phlebotomus (Sergentomyia) renauxi Parrot & Schwetz.

P. renauxi Parrot & Schwetz, 1937, *Rev. Zool. Bot. afr.* 29: 221.

Type locality Malda, Belgian Congo, type specimens in the Museum of the Belgian Congo, Tervueren. The description below is after Parrot & Schwetz.

♀. Length: 1.5-1.6 mm., hind leg 1.8-2 mm. Antenna: formula 2/III-XV, segment III (0.09-0.10 mm.) < IV + V, AIII/E = 0.62-0.64, ascoids on IV = 0.3 length of seg-

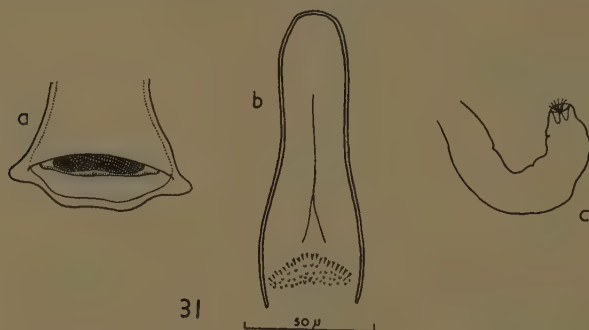


FIG. 31.—*P. renauxi*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. (After Parrot and Schwetz, 1937.)

ment. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 2.5, 3.5, 3.5, 6.3. *Epipharynx*: length 0.14 mm. *Buccal cavity*: with about 60 small and monomorphic teeth on an arc slightly concave posteriorly; pigmented plate very dark, oval, not reaching the lateral borders of the buccal cavity and with no anterior process. *Pharynx*: about 1.5 times as wide posteriorly as anteriorly and armed in its posterior part, the lateral borders of which are almost parallel, with about 60 short pointed teeth. *Wing*: length 1.3-1.4 mm., width 0.31-0.35 mm., alar index 0.61-0.66, delta + 0.018 to + 0.05 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. Unknown.

Distribution: BELGIAN CONGO.

Phlebotomus (Sergentomyia) antennatus Newstead.

P. antennatus Newstead, 1912, *Bull. ent. Res.* 3: 365.

P. antennatus Newstead, 1920, *ibid.* 11: 305.

P. minutus var. *antennatus* Newstead & Sinton, 1921, *Ann. trop. med. Parasit.* 15: 103

P. minutus var. *antennatus* Parrot, 1930, *Rev. Zool. Bot. afr.* 19: 181.

(nec) *P. minutus* var. *antennatus* Theodor, 1933, *Bull. ent. Res.* 24 : 539.

P. antennatus Parrot, 1942, *Arch. Inst. Pasteur Algér.* 20 : 322.

P. antennatus Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43 : 333.

Type specimens, from Salaga, Gold Coast, are in the British Museum.

P. antennatus was originally described by Newstead (1912, 1920) as a distinct species, but later Newstead and Sinton (1921) thought the evidence then available was insufficient to separate it from *P. minutus* and placed it as a variety of that species. Sinton (1933) later found that the differences between both male and female forms of Indian specimens were so great that he considered that *P. antennatus* should again be raised to specific rank, although the identity of the Indian forms with Newstead's African species was uncertain. With Parrot's (1942, 1943) re-description of *P. minutus* Rondani it is evident that the various forms regarded as *P. antennatus* can no longer be considered varieties of *P. minutus* Rondani, and the form described by Parrot (1930)

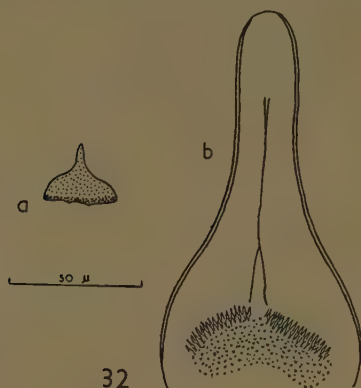


FIG. 32.—*P. antennatus*, ♀: a, pigmented area; b, pharynx. (After Parrot, 1930.)

from the Congo as *P. minutus* var. *antennatus* was regarded by that worker (1942) as *P. signatipennis*. In 1948 the writers were able to re-examine Newstead's African type specimens of *P. antennatus* and found that this form is closely related to *P. signatipennis*, *P. cinctus* and other forms given specific rank by Parrot (1943) when he found that they could no longer be regarded as varieties of *P. minutus*. In this work these and some allied forms are treated as varieties of *P. antennatus* Newstead. The subject is discussed more fully in the section on synonymy (page 407). The description of the female given below is Newstead's type series (holotype female and seven other female specimens).

♀. Length : 1.82 mm. Antenna : formula 2/III-XV, segment III (0.08 mm) < IV + V, AIII/E = 0.6, ascoids on IV = 0.5 length of segment. Palp : formula 1,2,(3,4),5, relative lengths 1, 3.2, 3.75, 3.75, 8.75. Epipharynx : length 0.14 mm. Buccal cavity : 26-28 pointed teeth on an arc concave posteriorly, the teeth being equal and monomorphic or a few of the median ones being slightly shorter than the others; pigmented plate helmet-shaped. Pharynx : about 2.5 times as broad posteriorly as anteriorly, cordiform,

but not extremely so, and bearing in its posterior part numerous strong spines like those of var. *signatipennis* and var. *cinctus*. *Wing*: length 1.22 mm., width 0.33 mm., alar index 0.43, delta + 0.03 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. The males of *P. antennatus* and its varieties are extremely difficult to differentiate and usually accurate determination can only be made by referring to the female specimens collected in association with them (Parrot, 1948). A specimen in the British Museum (Natural History) collected in Accra in June, 1919, and labelled by Newstead "*P. antennatus*, type ♂" agrees closely with the published descriptions of the males of var. *cinctus* and var. *signatipennis*, but we consider it unjustified to present a description of the male of *P. antennatus* as it is not known which, if any, of the males corresponds with Newstead's type female.

Distribution: NORTHERN ASHANTI, GOLD COAST, A.-E. SUDAN.

Phlebotomus (Sergentomyia) antennatus var. *signatipennis* Newstead.

P. signatipennis Newstead, 1920, *Bull. ent. Res.* 11: 305.

P. minutus var. *signatipennis* Theodor, 1933, *ibid.* 24: 537.

P. sanneri Gaillard & Nitzulescu, 1931, *Ann. Parasit. hum. comp.* 9: 233.

P. signatipennis Parrot, 1942, *Arch. Inst. Pasteur Algér.* 20: 322.

P. antennatus var. *signatipennis* Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43: 333.

Type specimens from Gambago, Gold Coast, are in the British Museum. The synonyms given above are discussed in the section on synonymy. The

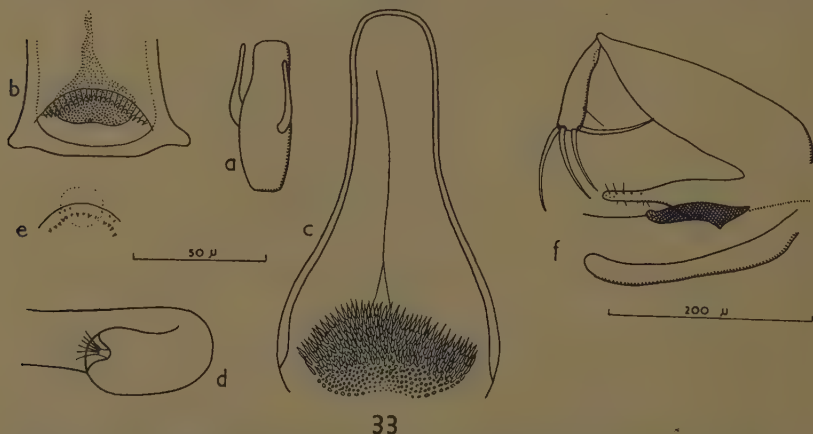


FIG. 33.—*P. antennatus* var. *signatipennis*, ♀: a, fourth antennal segment; b, buccal cavity; c, pharynx; d, spermatheca. ♂: e, buccal cavity; f, terminalia. (a, b, c and e after Parrot, 1948; d and f after Parrot, 1942.)

description below is largely after Parrot (1948) from specimens from the A.-E. Sudan (7 females and 33 males).

♀. *Length*: 1.7 mm., hind leg 2.0 mm. *Antenna*: formula 2/III-XV, segment III (0.08-0.1 mm.). < IV + V. AIII/E = 0.6-0.75, ascoids on IV = 0.4 length of segment. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 2.3, 3.7, 3.5, 7.3. *Epipharynx*: length 0.14-0.16 mm. *Buccal cavity*: with 22-26 sharp pointed teeth on an arc concave posteriorly; pigmented plate helmet-shaped. *Pharynx*: about 2.5 times as wide posteriorly as an-

teriorly and armed with numerous strong spines giving the appearance of a bilobed or heart-shaped brush. *Wing*: length 1.45–1.63 mm., width 0.31–0.36 mm., alar index 0.52–0.7, delta 0 to + 0.034 mm. *Spermactheca*: simple, tubular, of *minutus* type.

♂. *Length*: 1.6–1.9 mm., hind leg 1.8–2.14 mm. *Antenna*: formula 1/III–XV, segment III (0.09–0.11 mm.) < IV + V, AIII/E = 0.68–0.79, ascoid on IV = 0.4 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.4, 3.7, 3.6, 7. *Epipharynx*: length 0.13–0.14 mm. *Buccal cavity*: with 14–20 short pointed teeth, more or less equal, on an arc concave posteriorly and 6–16 anterior small punctiform denticles; pigmented area irregularly round or oval, sometimes absent. *Pharynx*: about 2.5 times as wide posteriorly as anteriorly, armed with faint oblique transverse ridges bearing fine punctiform spines. *Wing*: Length 1.3–1.5 mm., width 0.22–0.3 mm., alar index 0.33–0.64, delta + 0.017 to – 0.10. *Terminalia*: coxite (0.2–0.24 mm.) about 2.5 times as long as style (0.09–0.1 mm.), which bears four terminal spines and small ventral seta at 0.75; paramere 0.15–0.18 mm., penis sheath 0.08–0.10 mm., lateral lobe 0.17–0.23 mm.

In the female the number of buccal teeth in var. *signatipennis* is similar to that in var. *dubius*, but the two forms are readily separated by the marked inequality of these teeth, the ragged posterior margin of the pigmented plate and the very wide pharynx of var. *dubius*.

Distribution: GOLD COAST, IVORY COAST, DAHOMEY, FRENCH SUDAN, SENEGAL, GABON, BELGIAN CONGO, A.-E. SUDAN, ABYSSINIA, ERITREA.

Phlebotomus (Sergentomyia) antennatus var. *occidentalis* Theodor.

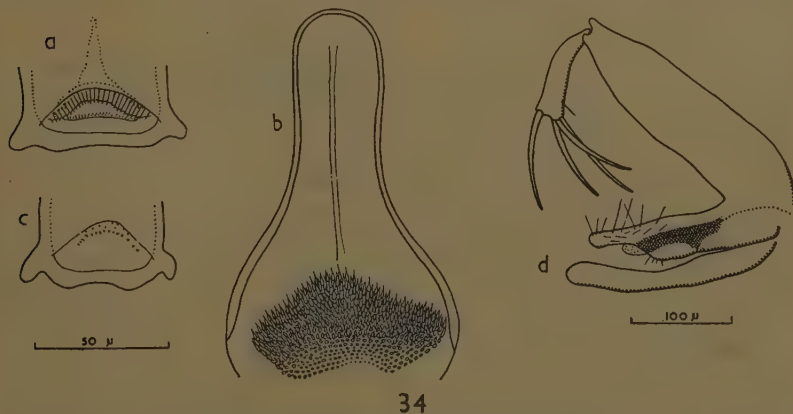
P. minutus var. *occidentalis* Theodor, 1933, *Bull. ent. Res.* 24: 537.

P. occidentalis Parrot, 1942, *Arch. Inst. Pasteur Algér.* 20: 322.

P. antennatus var. *occidentalis* Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43: 333.

Co-type specimens (2 ♀) are in the British Museum. The description of the female given below is mainly after Parrot.

♀. *Length*: 1.62–2.1 mm., hind leg 2.1–2.23 mm. *Antenna*: formula 2/III–XV, segment III (0.084–0.1 mm.) < IV + V, AIII/E = 0.58–0.68, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,(4,3),5, relative lengths 1, 2.3, 3.5, 3.45, 6. *Epipharynx*: length 0.13–0.14 mm. *Buccal cavity*: with 26–32 narrow, straight pointed teeth on an



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FIG. 34.—*P. antennatus* var. *occidentalis*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity; d, terminalia. (After Parrot, 1948.)

are concave posteriorly and sometimes small anterior punctiform denticles at the lateral borders; pigmented plate helmet-shaped. *Pharynx*: cordiform, resembling that of *P. antennatus* var. *signatipennis*. *Wing*: length 1.46–1.6 mm., width 0.31–0.38 mm., alar index 0.4–0.78, delta -0.034 to $+0.051$ mm. *Spermatheca*: tubular, of *minutus* type.

♂. As in *P. antennatus* var. *signatipennis*.

This variety differs from the other varieties of *P. antennatus* in the buccal teeth (24–32) which are very narrow, equal and on an arc less strongly concave than in the others.

Distribution: GOLD COAST, NIGERIA, A.-E. SUDAN.

Phlebotomus (Sergentomyia) antennatus var. *cinctus* Parrot & Martin.

P. cinctus Parrot & Martin, 1944, *Arch. Inst. Pasteur Algér.* 22: 55.

P. cinctus Parrot, 1948, *ibid.* 26: 259.

P. antennatus var. *cinctus* Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43: 333.

Type locality Djibouti, French Somaliland; type specimens in the Institut Pasteur d'Algérie. The description given below is mainly after Parrot (1948), from 53 males and 25 females.

♀. Length: 1.42–1.7 mm., hind leg 1.75–2 mm. *Antenna*: formula 2/III–XV, segment III (0.07–0.93 mm.) $< IV + V$, AIII/E = 0.47–0.65, ascoids on IV = 0.4 length

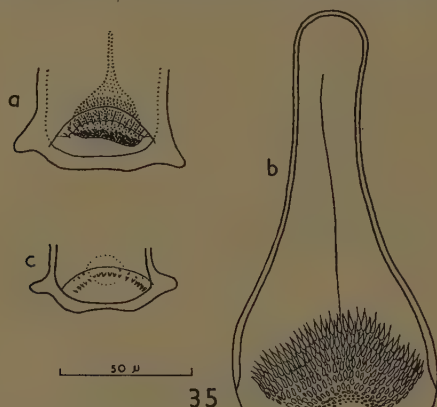


FIG. 35.—*P. antennatus* var. *cinctus*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity. (After Parrot, 1948.)

of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.3, 3.7, 3.4, 7.4. *Epipharynx*: length 0.14–0.17 mm. *Buccal cavity*: with 14–20 teeth and on each side a group of 5–8 anterior punctiform denticles; pigmented area helmet-shaped. *Pharynx*: about three times as wide posteriorly as anteriorly, cordiform, and armed with strong spines. *Wing*: length 1.3–1.5 mm., width 0.24–0.34 mm., alar index 0.42–0.83, delta -0.05 to $+0.034$ mm. *Spermatheca*: tubular of *minutus* type.

♂. As in *P. antennatus* var. *signatipennis*.

The female of var. *cinctus* differs from the other varieties of *P. antennatus* in the smaller number of buccal teeth (16–20) and the pharynx, less cordiform in shape, with fewer though stouter spines.

Distribution: FRENCH SOMALILAND, A.-E. SUDAN, UGANDA.

Phlebotomus (Sergentomyia) antennatus var. *dubius* Parrot, Mornet & Cadenat.

P. minutus var. *antennatus* Theodor, 1933, *Bull. ent. Res.* 24 : 539.

P. dubius Parrot, Mornet & Cadenat, 1945, *Arch. Inst. Pasteur Algér.* 23 : 232.

P. antennatus var. *dubius* Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43 : 333.

Type locality Senegal. The descriptions given here are after Parrot, Mornet and Cadenat. Type specimens in Institut Pasteur d'Algérie.

♀. Length : 1.9–2.12 mm., hind leg 2.1–2.46 mm. Antenna : formula 2/III–XV, segment III (0.1–0.11 mm.) < IV + V, AIII/E = 0.6–0.7, ascoids on IV = 0.5 length of segment. Palp : formula 1,2,(3,4),5, relative lengths 1, 2.6, 4.2, 4.2, 8.7. Epipharynx : length 0.16–0.18 mm. Buccal cavity : with 24–28 teeth on an arc concave posteriorly, the six median ones and the 2–3 extreme lateral ones on each side being smaller than the inter-

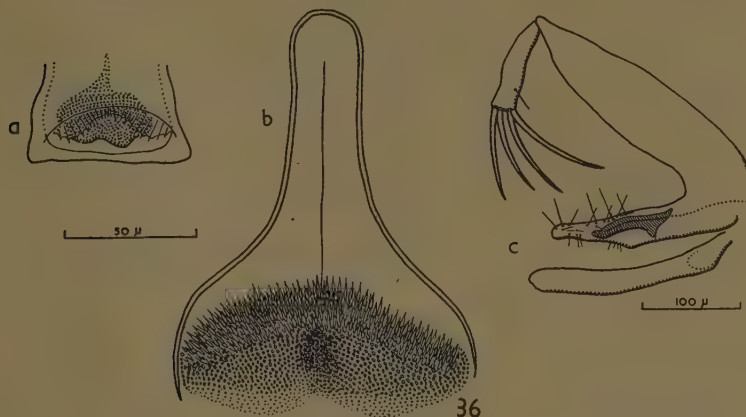


FIG. 36.—*P. antennatus* var. *dubius*, ♀: a, buccal cavity; b, pharynx. ♂: c, terminalia. (After Parrot, Mornet and Cadenat, 1945.)

vening ones, and with a group of 6–8 small anterior punctiform denticles on both sides; pigmented area helmet-shaped, with irregular posterior margin. Pharynx : about four times as wide posteriorly as anteriorly, markedly cordiform, with a prominent armature of many long spines. Wing : length 1.5–1.66 mm., width 0.34–0.4 mm., alar index 0.55–0.77, delta + 0.03 to + 0.08 mm. Spermatheca : simple, of *minutus* type.

♂. Length : 1.8–2.1 mm., hind leg 2–2.15 mm. Antenna : formula 1/III–XV, segment III (0.11–0.12 mm.) < IV + V, AIII/E = 0.72–0.82, ascoid on IV = 0.35 length of segment. Palp : formula 1,2,(3,4),5, relative lengths 1, 2.6, 4.1, 4.2, 8.6. Epipharynx : length 0.14–0.16 mm. Buccal cavity : with 14–16 poorly developed irregular teeth on an arc concave posteriorly, the 3–4 median teeth being smaller than the lateral ones, and with a row of 8–10 anterior punctiform denticles; pigmented area irregular, sometimes absent. Pharynx : about twice as wide posteriorly as anteriorly, bearing some transverse ridges with fine short spines. Terminalia : coxite (0.24–0.27 mm.) 2.5 times as long as style, which bears four terminal spines and small non-deciduous seta at 0.75; paramere (0.17–0.19 mm.) blunt, penis sheath (0.08–0.09 mm.) finger-shaped, lateral lobe (0.19–0.22 mm.) longer than paramere.

The female of var. *dubius* differs from the other varieties of *P. antennatus* in the very wide cordiform pharynx, the morphology of the buccal cavity with

24-28 teeth, the median ones markedly smaller than the others, and the pigmented area with ragged posterior margin.

Distribution: GOLD COAST, SENEGAL, FRENCH SUDAN, FRENCH GUINEA, IVORY COAST.

Phlebotomus (Sergentomyia) bedfordi Newstead.

P. bedfordi Newstead, 1914, *Bull. ent. Res.* 5: 191.

P. bedfordi Parrot, 1921, *Arch. Inst. Pasteur Afr. N.* 1: 269.

P. congolensis var. *distinctus* Theodor, 1933, *Bull. ent. Res.* 24: 542.

P. bedfordi Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43: 333.

Type locality Onderstepoort, Transvaal; type specimen in the British Museum. The description of the female given below is from Newstead's type specimen, that of the male from Sudan specimens determined as *P. congolensis* var. *distinctus*, partly after Parrot (1948).

♀. Length: 2.54 mm. Antenna: formula 2/III-XV, segment III (0.16 mm.) < IV + V, AIII/E = 0.76, ascoids on IV = 0.5 length of segment. Palp: formula 1,2,3,(4,5),

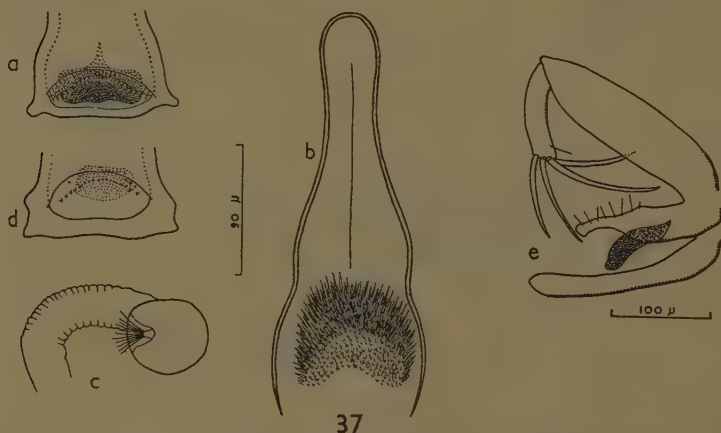


FIG. 37.—*P. bedfordi*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (a, b, c and e from Sudan specimens; d after Parrot, 1948.)

relative lengths 1, 3.75, 4.75, 6.25, 6.25. *Buccal cavity*: with about 22 pointed teeth on an arc concave posteriorly, the 7-8 median teeth being smaller than the lateral ones; pigmented area with slightly irregular posterior margin. *Pharynx*: more than twice as wide posteriorly as anteriorly, constricted in its broad posterior portion, which is armed with numerous strong spines, the anterior margin of the armed area being convex anteriorly. *Wing*: length 1.91 mm., width 0.53 mm., alar index 0.8, delta + 0.05 mm. *Spermatheca*: not visible, hence presumably thin-walled and tubular.

♂. Length: 1.8-2.5 mm. Antenna: formula 1/III-XV, segment III (0.1-0.15 mm.) < IV + V, AIII/E = 0.7-0.94, ascoid on IV = 0.3 length of segment. Palp: formula 1,2,3,4,5, relative lengths 1, 2.7, 4.3, 4.8, 9.8. *Epipharynx*: length 0.15-0.17 mm. *Buccal cavity*: with about 20 teeth on an arc concave posteriorly, the median 6-8 being shorter and narrower than the lateral ones, and an irregular and variable row of anterior punctiform denticles; pigmented area irregularly oval with small anterior prolongation.

Pharynx: about 1.5 times as wide posteriorly as anteriorly, armed with pointed teeth and, more posteriorly, transverse ridges. *Wing*: length 1.5–1.6 mm., width 0.32–0.4 mm., alar index 0.35–0.7, delta -0.05 to $+0.07$ mm. *Terminalia*: coxite (0.22–0.28 mm.) 2.5 times as long as style (0.1–0.11 mm.) which bears four spines and small non-deciduous seta at 0.8; paramere (0.16–0.20 mm.) with blunt tip, penis sheath (0.09 mm.) finger-shaped, strongly curved, with a subapical dorsal indentation, so that the distal extremity appears upturned as a sort of terminal lobe; lateral lobe 0.19–0.25 mm.

Distribution: TRANSVAAL, A.-E. SUDAN, GOLD COAST, NIGERIA, SENEGAL, FRENCH GUINEA, DAHOMEY, KENYA, UGANDA.

Phlebotomus (Sergentomyia) bedfordi var. *congolensis* Bequaert & Walravens.

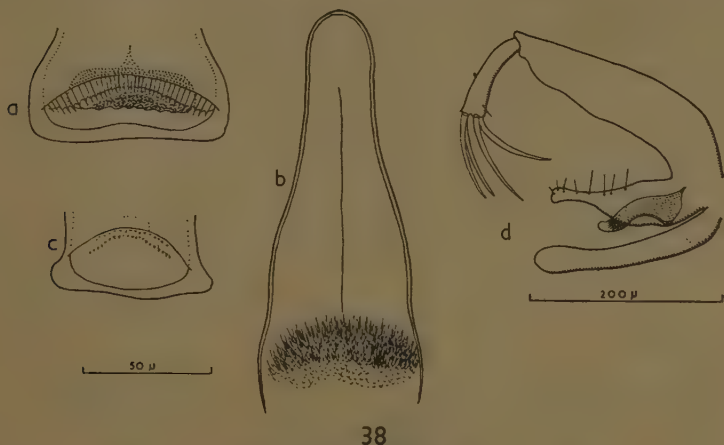
P. africanus var. *congolensis* Bequaert & Walravens, 1930, *Rev. Zool. Bot. afr.* 19: 38.

P. nairobiensis Theodor, 1931, *Bull. ent. Res.* 22: 472.

P. congolensis Parrot, 1933, *Rev. Zool. Bot. afr.* 23: 239.

P. congolensis Theodor, 1933, *Bull. ent. Res.* 24: 537.

Type locality Katanga, Belgian Congo. The description below is largely after Bequaert and Walravens except as regards the buccal cavity of the female, about which there is some discrepancy between the text and the illustration.



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FIG. 38.—*P. bedfordi* var. *congolensis*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity; d, terminalia. (a and b from Sudan specimens; c after Parrot, 1948; d after Theodor, 1931.)

♀. Length: 2.2–2.2 mm. Antenna: formula 2/III–XV, segment III (0.15 mm.) < IV + V, AIII/E = 0.8–0.9, ascoids on IV = 0.5 length of segment. Palp: formula 1,2,3,4,5, relative lengths 1, 2.1, 2.7, 3.4, 7.2. Epipharynx: length 0.17 mm. Buccal cavity: with 34–40 teeth on an arc concave posteriorly, the median 20 teeth being slightly smaller than the lateral ones; pigmented area roughly oval with ragged posterior margin and small anterior prolongation. Pharynx: 3–4 times as wide posteriorly as anteriorly, more heavily armed than in *P. bedfordi*, with less marked constriction in its posterior part. Wing: length 1.4–2 mm., width 0.35–0.4 mm., alar index 0.45–0.8, delta $+0.05$ to -0.03 mm. Spermatheca: tubular, of *minutus* type.

♂. *Length*: 2.0-2.3 mm. *Antenna*: formula 1/III-XV, segment III (0.15 mm.) < IV + V, AIII/E = I, ascoid on IV = 0.34 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.1, 3.3, 3.9, 7.5. *Epipharynx*: length 0.15 mm. *Buccal cavity*: with 25-30 fine pointed teeth on an arc concave posteriorly, median teeth slightly smaller than lateral ones; pigmented plate small, oval, often absent. *Pharynx*: with some fine point-like teeth and transverse folds. *Terminalia*: coxite (0.5 mm.) more than 2.5 times as long as style (0.17 mm.), which bears four terminal spines and small ventral seta at 0.8; paramere 0.33 mm., penis sheath (0.17 mm.) finger-shaped, curved, with a small up-turned terminal lobe; lateral lobe 0.37 mm.

This variety differs from *P. bedfordi* in the greater number and more uniform size of the buccal teeth, wider and more heavily armed pharynx in the female; in the male AIII is as long as or longer than the epipharynx whereas in *P. bedfordi* it is constantly shorter.

Distribution: ABYSSINIA, A.-E. SUDAN, EAST AFRICA, BELGIAN CONGO, SOUTHERN RHODESIA, TRANSVAAL, UGANDA.

Phlebotomus (Sergentomyia) bedfordi var. *firmatus* Parrot & Malbrant.

P. congolensis var. *firmatus* Parrot & Malbrant, 1945, *Arch. Inst. Pasteur Algér.* 23: 121.

P. bedfordi var. *firmatus* Kirk & Lewis, 1949, *Ann. trop. Méd. Parasit.* 43: 333.

Type specimens in the Institut Pasteur d'Algérie. The descriptions are after Parrot and Malbrant, from 16 females and 12 males from Brazzaville, Makawa and Ouessa, Middle Congo.

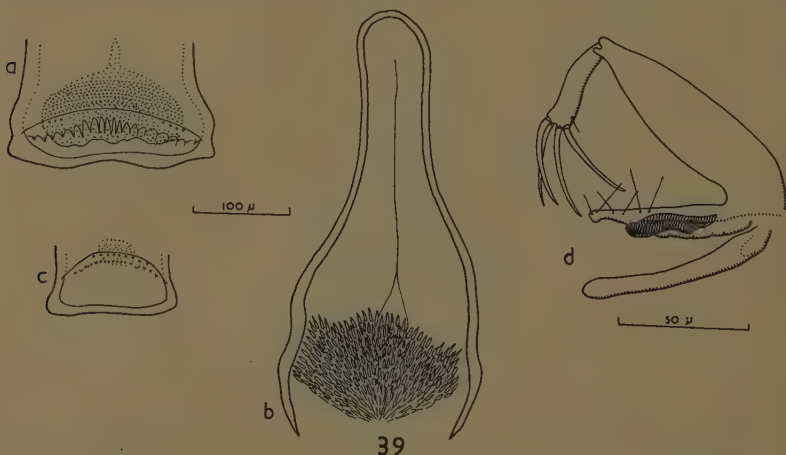


FIG. 39.—*P. bedfordi* var. *firmatus*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity; d, terminalia. (After Parrot and Malbrant, 1945.)

♀. *Length*: 1.84-2.15 mm., hind leg 2.3-2.5 mm. *Antenna*: formula 2/III-XV, segment III (0.13-0.14 mm.) < IV + V, AIII/E = 0.8-0.9, ascoids on IV = 0.7 length of segment. *Palp*: formula 1,2,3,4,5. *Epipharynx*: length 0.16-0.17 mm. *Buccal cavity*: with 16-20 pointed teeth, the 4-6 median teeth being straighter and the extreme lateral ones shorter, than the intermediate ones; pigmented plate with irregular posterior margin and faint anterior prolongation. *Pharynx*: about three times as wide posteriorly as anteriorly, with a constriction in its wide posterior part, which bears numerous strong

spines terminating in fine slender prolongations, anterior margin of armed area strongly convex anteriorly. *Wing*: length 1.53–1.63 mm., width 0.37–0.43 mm., alar index 0.65–0.94, delta + 0.1 to + 0.14 mm. *Spermathaca*: tubular, of *minutus* type.

♂. *Length*: 1.9–2.0 mm., hind leg 2.2–2.4 mm. *Antenna*: formula 1/III–XV, segment III (0.14–0.17 mm.) < IV + V, AIII/E = 1.1–1.2, ascoid on IV = 0.5 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.9, 4.4, 6.1, 9.7. *Epipharynx*: length 0.14–0.16 mm. *Buccal cavity*: 14–18 pointed and irregular teeth on an arc slightly concave posteriorly, the 6–8 median ones slightly smaller than the lateral ones; a variable row of small anterior punctiform denticles; pigmented area irregularly oval, sometimes absent. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with some fine ridges bearing small spines. *Wing*: length 1.5–1.6 mm., width 0.3–0.4 mm., alar index 0.38–0.75, delta – 0.03 to + 0.08 mm. *Terminalia*: coxite (0.2–0.24 mm.) about 2.4 times as long as style, which bears two terminal and two subterminal spines with small ventral seta at 0.9; paramere 0.15–0.17 mm. penis sheath (0.08–0.09 mm.) blunt, finger-shaped and curved, lateral lobe 0.17–0.20 mm.

This variety is distinguished by the relatively long ascoids in both sexes and the smaller number of buccal teeth in the female; in the male the number of buccal teeth is less than in var. *congolensis* whereas AIII is = or > IV + V.

Distribution: FRENCH CONGO.

Phlebotomus (Sergentomyia) bedfordi var. *medius* Kirk & Lewis.

P. congolensis var. *medius* Kirk & Lewis, 1950, *Proc. R. ent. Soc. Lond. (B)* 19: 11.

P. bedfordi var. *medius* Kirk & Lewis, 1949, *Ann. trop. Med. Parasit.* 43: 333.

Type specimens in the British Museum. The description below is based on 9 males and 12 females from Bwamba, Uganda, after Kirk and Lewis.

♀. *Length*: 2.0–2.4 mm. *Antenna*: formula 2/III–XV, segment III (0.12–0.14 mm.) < IV + V, AIII/E = 0.73–0.87, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.3, 3.4, 5, 8.8. *Epipharynx*: length 0.13–0.15 mm. *Buccal cavity*: 30–35 pointed teeth on an arc concave posteriorly, the median teeth being shorter than the lateral ones which incline slightly inwards towards the mid-line; pigmented area helmet-shaped. *Pharynx*: about twice as wide posteriorly as anteriorly with a constriction

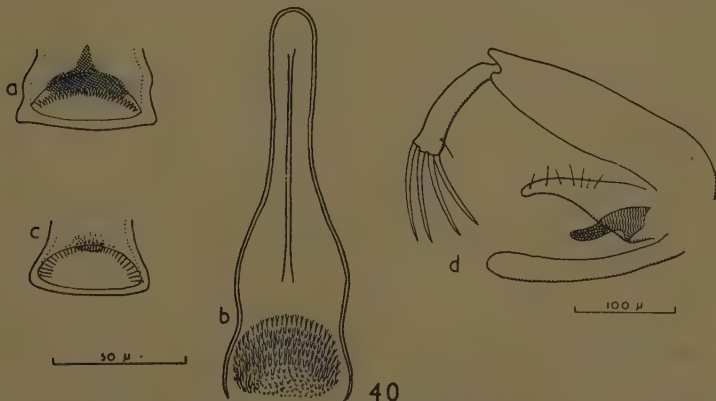


FIG. 40.—*P. bedfordi* var. *medius*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity; d, terminalia. (After Kirk and Lewis, 1950.)

in its expanded part which bears numerous well-developed pointed spines. *Wing*: length 1.45–1.6 mm., width 0.38–0.42 mm., alar index 0.84–1, delta + 0.1 to + 0.12 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. *Length*: 2.0–2.35 mm. *Antenna*: formula 1/III–XV, segment III (0.13–0.15 mm.) < IV + V, AIII/E = 0.8–1, ascoid on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.7, 3.5, 4.3, 8.6. *Epipharynx*: length 0.13–0.18 mm. *Buccal cavity*: with about 35 pointed teeth on an arc concave posteriorly, the median teeth shorter and straighter than the lateral ones; anterior to this a row of ill-defined denticles; pigmented area small, irregular, sometimes absent. *Pharynx*: about 1.5 times as wide posteriorly as anteriorly, armed with irregular rows of small punctiform teeth. *Wing*: length 1.35 mm., width 0.3 mm., alar index 0.8, delta + 0.05 mm. *Terminalia*: coxite (0.2–0.27 mm.) more than twice as long as style, which bears four terminal spines and small ventral seta at 0.8; paramere (0.14–0.20 mm.) with blunt tip; penis finger-shaped, strongly curved with blunt extremity; lateral lobe 0.17–0.23 mm.

This variety differs from var. *firmatus* in the short ascoids in both sexes. The pharynx in the female is much less heavily armed than in var. *congolensis*, and rather resembles *P. bedfordi*, but the buccal cavity is quite unlike that of *P. bedfordi*.

Distribution: UGANDA.

Phlebotomus (Sergentomyia) cowlandi Lewis & Kirk.

P. cowlandi Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond. (B)* 15: 155.

This species is known by a single male specimen from Gallabat, A.-E. Sudan. The type specimen is in the British Museum.

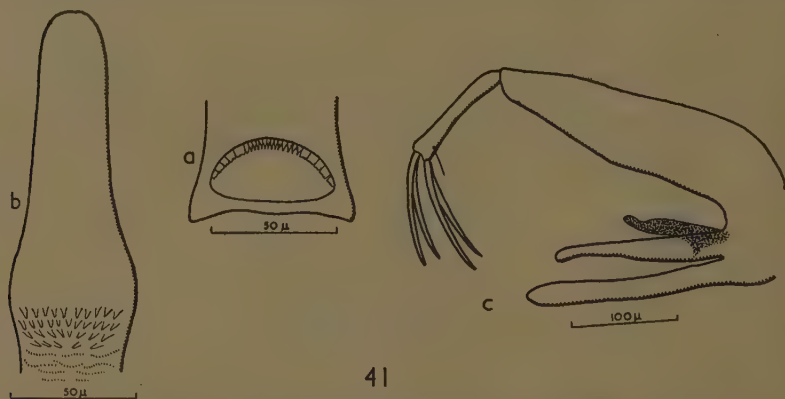


FIG. 41.—*P. cowlandi*, ♂: a, buccal cavity; b, pharynx; c, terminalia. (After Lewis and Kirk, 1946.)

♀. Unknown.

♂. *Length*: 2.0 mm. *Antenna*: formula 1/III–XV, segment III (0.13 mm.) < IV + V, AIII/E = 0.9, ascoid on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.7, 4, 5.1, 8.3. *Epipharynx*: length 0.17 mm. *Buccal cavity*: with 25 teeth on an arc strongly concave posteriorly, the outer five teeth on either side broad and each with several points, the central teeth narrow and pointed; no pigmented area. *Pharynx*: 1.5 times as wide posteriorly as anteriorly, armed with broad teeth and minute

spicules posteriorly. *Wing*: length 1.4 mm., width 0.35 mm., alar index 0.5, delta + 0.03 mm. *Terminalia*: coxite (0.26 mm.) 2.5 times as long as style (0.1 mm.), which bears four terminal spines and small ventral seta at 0.9; paramere (0.19 mm.) blunt; penis sheath (0.08 mm.) finger-shaped and blunt with notch near the tip; lateral lobe 0.21 mm.

Theodor (1948) considers this species may be identical with *P. bedfordi* var. *congolensis*.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) richardi Parrot & Wanson.

P. richardi Parrot & Wanson, 1946, *Rev. Zool. Bot. afr.* 39: 225.

This species is known from one female only, from Duma, Belgian Congo. Type specimen in the Museum of the Belgian Congo, Tervueren. The description below is after Parrot and Wanson.

♀. *Length*: 1.77 mm., hind leg 2.5 mm. *Antenna*: formula 2/III-XV, segment III (0.14 mm.) < IV + V, AIII/E = 1, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3, 4.3, 5.9, 7. *Epipharynx*: length 0.14 mm. *Buccal*

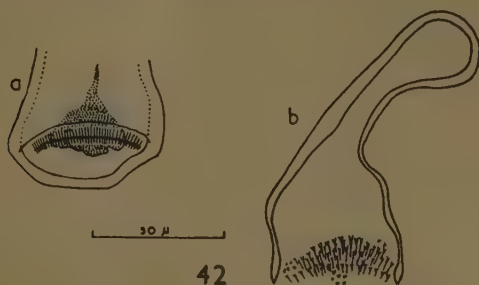


FIG. 42.—*P. richardi*, ♀: a, buccal cavity; b, pharynx. (After Parrot and Wanson, 1946.)

cavity: with 40 pointed monomorphic teeth on an arc concave posteriorly; pigmented plate roughly helmet-shaped with ragged posterior margin. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with numerous spines with wide bases and fine, backwardly pointing extremities, the anterior margin of the armed area being convex anteriorly. *Wing*: length 1.56 mm., width 0.43 mm., alar index 1.0, delta + 0.032 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. Unknown.

This species resembles *P. pastorianus*, but differs in its smaller size, alar index, the greater number of the buccal teeth and the general arrangement of the pharyngeal armature.

Distribution: BELGIAN CONGO, UGANDA.

Phlebotomus (Sergentomyia) schoutedeni Adler, Theodor & Parrot.

P. schoutedeni Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18: 72.

Type locality Stanleyville, Belgian Congo, types and co-types in the Hebrew University, Jerusalem and the Institut Pasteur d'Algérie. The description given below is after Adler, Theodor and Parrot, based on 61 females and 97 males.

♀. Length : 1.5–1.9 mm., hind leg 2.2–2.4 mm. Antenna : formula 2/III–XV, segment III (0.11–0.13 mm.) < IV + V, AIII/E = 0.6–0.7, ascoids on IV = 0.43 length of segment. Palp : formula 1,2,3,4,5, relative lengths 1, 2.5, 3.5, 4, 7.1. Epipharynx : length 0.19–0.20 mm. Buccal cavity : with about 20 pointed teeth on an arc concave posteriorly, the 8 median teeth being smaller and straighter than the lateral ones, pigmented area dark brown, elliptical. Pharynx : about twice as wide posteriorly as anteriorly and armed with numerous strong teeth. Wing : length 1.4–1.6 mm., width 0.35–0.37 mm., alar index 0.5–0.83, delta + 0.1 to + 0.15 mm. Spermatheca : simple, tubular.

♂. Length : 1.4–1.8 mm., hind leg 2.1–2.4 mm. Antenna : formula 1/III–XV, segment III (0.13–0.17 mm.) < IV + V, AIII/E = 0.88–0.91, ascoid on IV = 0.25 length of

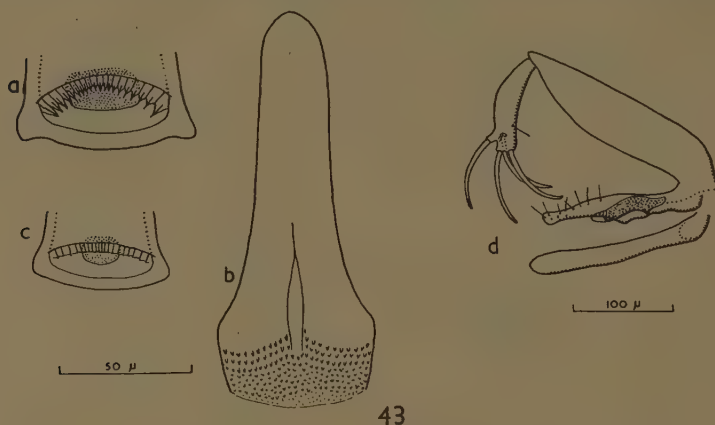


FIG. 43.—*P. schoutedeni*, ♀; *a*, buccal cavity; *b*, pharynx. ♂: *c*, buccal cavity; *d*, terminalia. (After Adler, Theodor and Parrot, 1929.)

segment. Palp : formula 1,2,3,4,5, relative lengths 1, 2.3, 3.4, 4.0, 8.0. Epipharynx : length 0.15–0.18 mm. Buccal cavity : teeth as in the female but smaller and arranged in a less concave arc; pigmented plate also smaller and almost circular. Pharynx : about twice as wide posteriorly as anteriorly, teeth much less marked than in the female, small and pointed, arranged in rows in the posterior part of the organ. Wing : length 1.3–1.6 mm., width 0.27–0.32 mm., alar index 0.56–0.8, delta 0 to + 0.09 mm. Terminalia : coxite (0.21–0.24 mm.) slightly more than twice length of style (0.09–0.10 mm.), which bears four spines, two terminal and two sub-terminal, and small ventral seta at 0.7; paramere (0.23 mm.) blunt; penis sheath curved and finger-shaped (0.075 mm.), lateral lobe (0.26 mm.) longer than paramere.

Distribution : BELGIAN CONGO, UGANDA, TRANSVAAL, A.-E. SUDAN, DAHOMEY.

Phlebotomus (Sergentomyia) schoutedeni var. *pungens* Parrot.

P. schoutedeni var. *pungens* Parrot, 1948, Arch. Inst. Pasteur Algér. 26 : 145.

Type specimen in the British Museum. The following description is after Parrot, from seven females from the type locality, Li Rangu, A.-E. Sudan.

♀. Length : 1.81–2.13 mm., hind leg 2.45 mm. Antenna : formula 2/III–XV, segment III (0.1–0.13 mm.) < IV + V, AIII/E = 0.5–0.6, ascoid on IV = 0.2 length of segment.

Palp: formula 1,2,3,4,5, relative lengths 1, 3.1, 4.2, 4.6, 9.2. *Epipharynx*: length 0.2–0.22 mm. *Buccal cavity*: with 18–20 pointed teeth, the median two or three shorter and straighter than the lateral ones, pigmented area dark, oval, with small anterior prolongation. *Pharynx*: twice as wide posteriorly as anteriorly, armed with numerous strong spines in a transverse band. *Wing*: length 1.46–1.7 mm., width 0.32–0.44 mm., alar index 0.41–0.68, delta + 0.01 to + 0.07 mm.

♂. Unknown.

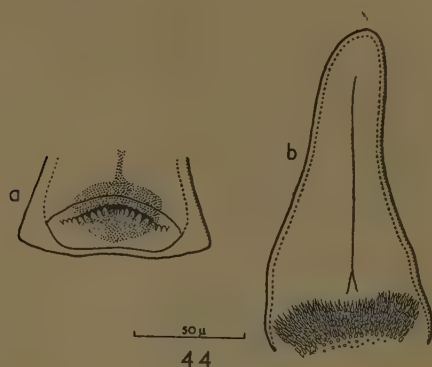


FIG. 44.—*P. schoutedeni* var. *pungens*, ♀: a, buccal cavity; b, pharynx. (After Parrot, 1948.)

This variety is distinguished from the typical *P. schoutedeni* by the greater uniformity of the buccal teeth, the wider and more heavily armed pharynx, and the greater size.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) yusafi Sinton.

P. yusafi Sinton, 1930, *Indian J. med. Res.* 18: 181.

Type locality Mombasa; type specimens in the British Museum. The description below has been abstracted from Sinton's paper, based on two females and one male.

♀. *Length*: 2.2 mm. *Antenna*: formula 2/III–XV, segment III (0.1–0.13 mm.) < IV + V, AIII/E = 0.61–0.81, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.6, 4.5, 8.9. *Epipharynx*: length 0.165–0.171 mm. *Buccal cavity*: with about 25 equal pointed teeth on an arc strongly concave posteriorly and a large dark pigmented area with anterior prolongation and ragged posterior margin. *Pharynx*: less than twice as wide posteriorly as anteriorly, pharyngeal armature well-developed and consists of a series of long posteriorly directed spines, those of the posterior part being slender and widely spaced, while the more anterior ones, arising from a dark stained area, are stouter and placed very close together. *Wing*: length 1.48–1.51 mm., width 0.4–0.43 mm., alar index 0.66, delta + 0.064 to + 0.085 mm. *Spermatheca*: simple, tubular, with wide duct.

♂. *Length*: 2.0 mm. *Antenna*: formula 1/III–XV, segment III (0.123 mm.) < IV + V, AIII/E = 0.87, ascoid on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.5, 4.3, 8.6. *Epipharynx*: length 0.14 mm. *Buccal cavity*: with

about 14 small atrophied teeth and a small, irregular pigmented area. *Pharynx*: about 1.2 times as wide posteriorly as anteriorly, armed with a few toothed ridges and some lines of small teeth posteriorly. *Wing*: length 1.3 mm., width 0.36 mm., alar index 0.55, delta + 0.028 mm. *Terminalia*: coxite (0.2) mm. 2.5 times as long as style (0.081 mm.),

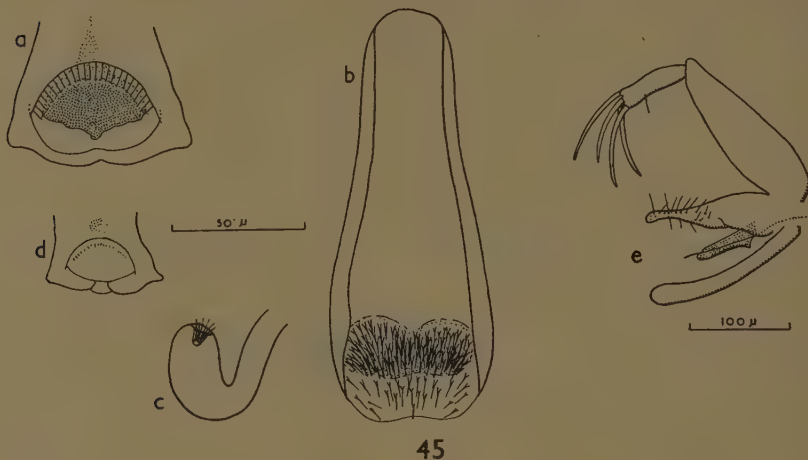


FIG. 45.—*P. yusafi*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. (After Sinton, 1930.)

which bears four curved spines, all terminal, and small non-deciduous seta at 0.6; paramere 0.165 mm.; penis sheath (0.123 mm.) with broad, bluntly rounded extremity; lateral lobe 0.17 mm.

Distribution: KENYA, A.-E. SUDAN.

Phlebotomus (Sergentomyia) pastorianus Parrot, Mornet & Cadenat.

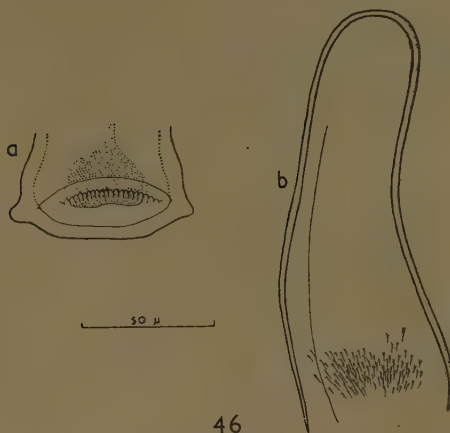
P. pastorianus Parrot, Mornet & Cadenat, 1945, *Arch. Inst. Pasteur Algér.* 23: 281.

This species is at present known from one female only from French Guinea. The description below is after Parrot, Mornet and Cadenat. Type specimen in Institut Pasteur d'Algérie.

♀. *Length*: 2.2 mm. *Antenna*: formula 2/III-XII (distal segments missing), segment III (0.135 mm.) < IV + V, AIII/E = 0.85, ascoids on IV = 0.6 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.7, 4.8, 8.6. *Epipharynx*: length 0.162 mm. *Buccal cavity*: with 21 pointed monomorphic teeth on an arc concave posteriorly; pigmented area helmet-shaped. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with numerous poorly developed spines, ending in long filiform points, the armed area being in the form of a triangle with the base directed anteriorly and widely separated from the sides of the pharynx. *Wing*: length 1.74 mm., width 0.51 mm., alar index 0.64, delta + 0.012 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. Unknown.

Distribution: FRENCH GUINEA.



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FIG. 46.—*P. pastorianus*, ♀: a, buccal cavity; b, pharynx. (After Parrot, Mornet and Cadenat, 1945.)

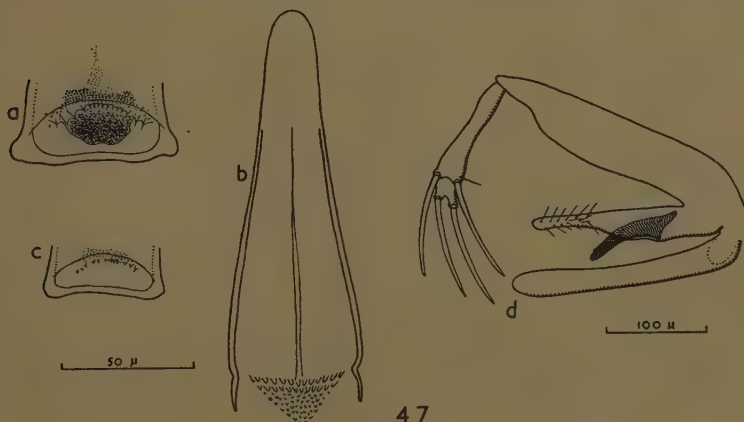
Phlebotomus (Sergentomyia) buxtoni Theodor.

P. buxtoni Theodor, 1933, *Bull. ent. Res.* 24: 544.

P. mathisi Parrot, 1935, *Arch. Inst. Pasteur Algér.* 13: 259.

Type locality Gold Coast (Tamale). The description is mainly after Theodor from one female and two males, supplemented from Parrot's (1935) descriptions of *P. mathisi* and *P. buxtoni* (Parrot, Mornet & Cadenat, 1945) from 42 males and 53 females.

♀. Length: 2.45 mm. Antenna: formula 2/III-XV, segment III (0.15-0.18 mm.) < IV + V, AIII/E = 0.65-0.8, ascoids on IV = 0.5 length of segment. Palp: formula



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FIG. 47.—*P. buxtoni*, ♀: a, buccal cavity; b, pharynx. ♂: c, buccal cavity; d, terminalia. (a and c after Parrot, Mornet and Cadenat, 1945; b and d after Theodor, 1933.)

1,2,(3,4),5, relative lengths 1, 2.3, 3.4, 3.5, 4.5. *Epipharynx*: length 0.22–0.24 mm. *Buccal cavity*: with 13–16 teeth on an arc concave posteriorly, the 4–8 median teeth narrow and parallel to axis of body, the 4 lateral teeth on each side large and point inwards as well as backwards; small punctiform denticles may be seen laterally; pigmented area irregular with anterior prolongation and ragged posterior margin. *Pharynx*: twice as wide posteriorly as anteriorly and with an armature of short stumpy teeth. *Wing*: length 1.95 mm., width 0.49 mm., alar index 0.9, delta + 0.09 mm. *Spermatheca*: simple, tubular, of *minutus* type.

♂. *Length*: 2.0–2.3 mm. *Antenna*: formula 1/III–XV, segment III (0.17–0.18 mm.) < IV + V, AIII/E = 0.8–0.9, ascoid on IV = 0.4 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.6, 4, 4.2, 9. *Epipharynx*: length 0.19–0.20 mm. *Buccal cavity*: with 14–17 teeth on an arc slightly concave posteriorly, the lateral teeth larger than the median ones and pointing slightly medially; additional punctiform teeth may be seen laterally; pigmented plate faint or absent. *Pharynx*: slender, with no distinct armature. *Terminalia*: coxite (0.27 mm.) about twice as long as style (0.12 mm.) which bears two long terminal spines and two markedly subterminal ones and small non-deciduous seta at 0.8; paramere (0.19 mm.) with blunt end; penis sheath (0.11 mm.) blunt, finger-shaped, curved downwards; lateral lobe 0.24 mm.

Distribution: GOLD COAST, DAKAR, A.-E. SUDAN.

Phlebotomus (Sergentomyia) aretasi Kervran.

P. aretasi Kervran, 1946, *Ann. Parasit. hum. comp.* 21: 155.

This species is known by one male only, from Bamako (Point G), French Sudan, and the description below is after Kervran.

♀. Unknown.

♂. *Length*: 2.5 mm. *Antenna*: formula 1/III–XV, segment III (0.28 mm.) > IV + V, AIII/E = 1.6, ascoid on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 1.8, 2.6, 3.5, 5.8. *Epipharynx*: length 0.175 mm. *Buccal cavity*: with about 16–18 irregular teeth with milled or serrated edges, pigmented plate dark brown, roughly

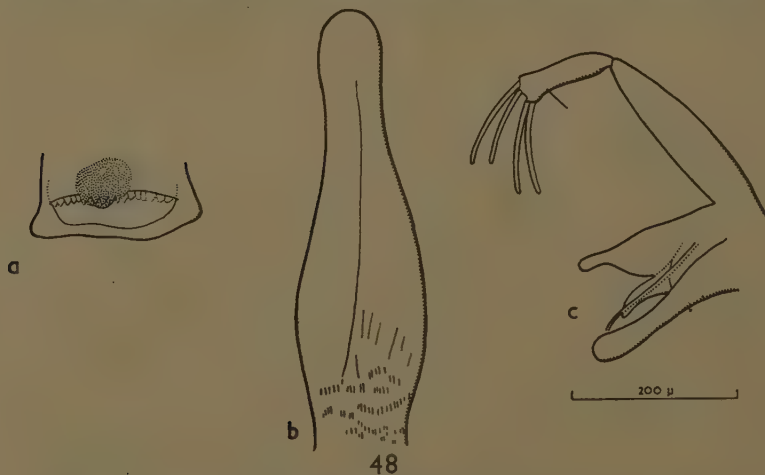


FIG. 48.—*P. aretasi*, ♂: a, buccal cavity; b, pharynx; c, terminalia. (After Kervran, 1946.)

quadrilateral. *Pharynx*: twice as wide posteriorly as anteriorly and armed with fine longitudinal spines arranged in groups of 4 or 5. *Wing*: length 2.0 mm., width 0.57 mm., alar index 1.1, delta + 0.24 mm., $\pi = + 0.05$ mm. *Terminalia*: coxite (0.23 mm., about 2.5 times length of style (0.095 mm.) which bears four terminal spines and small ventral seta at 0.6; paramere (0.21 mm.) with very wide base and hooked extremity; penis sheath (0.068 mm.) conical lateral lobe (0.23 mm.) same length as coxite.

Distribution: FRENCH SUDAN.

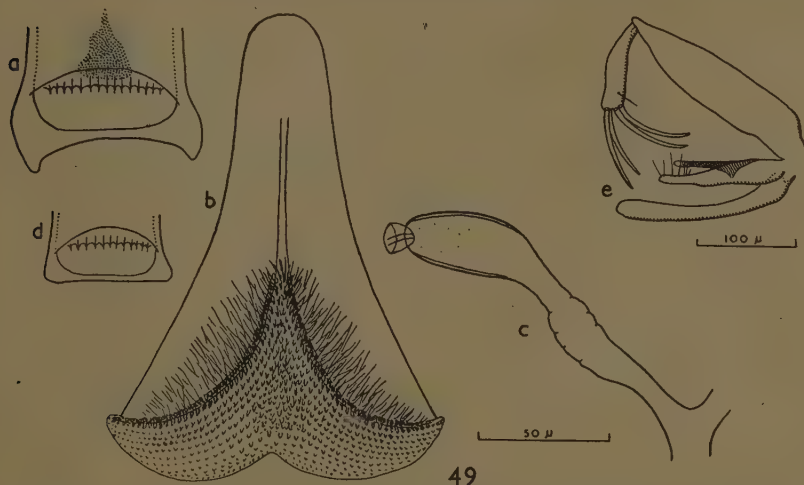
Phlebotomus (Sergentomyia) simillimus Newstead.

P. simillimus Newstead, 1914, *Bull. ent. Res.* 5: 180.

P. brodeni Parrot, 1930, *Rev. Zool. Bot. afr.* 19: 185.

P. simillimus Theodor, 1931, *Bull. ent. Res.* 22: 475; 1938, *ibid.* 29: 171.

Type locality Kintampo, Northern Ashanti, type specimens in the British Museum. The descriptions below are partly after Theodor, supplemented from our own material. The antennal formula is different from that given by Newstead (1914) and Parrot (1940). Theodor omits this character.



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FIG. 49.—*P. simillimus*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (a and d after Parrot, Mornet and Cadenat, 1945; b and e after Theodor, 1931; c after Parrot, 1930.)

♀. Length: 1.8–1.9 mm. *Antenna*: formula 2/III–XV, segment III (0.32–0.34 mm.) < IV + V, AIII/E = 1.66, ascoids on IV = 0.4 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.8, 4.7, 9.7. *Epipharynx*: length 0.19–0.20 mm. *Buccal cavity*: with 18–20 teeth with short points on an arc concave posteriorly; no pigmented plate. *Pharynx*: heart-shaped, five times as wide posteriorly as anteriorly, bearing a great number of very fine pointed teeth standing on pigmented areas. *Wing*: length 1.76–1.85 mm., width 0.54–0.55 mm., alar index 1.3–1.4, delta + 0.25 to 0.29 mm. *Spermathecae*: elliptical capsules with wide ducts.

♂. Length: 1.8–2.3 mm. *Antenna*: formula 1/III–XV, segment III (0.28–0.38 mm.) < IV + V, AIII/E = 1.8–2.2, ascoid on IV = 0.5 length of segment. *Palp*: formula

1,2,3,4,5, relative lengths 1, 3.3, 5, 6.2, 9.8. *Buccal cavity*: about 18 teeth with short points; no pigmented area. *Pharynx*: about twice as wide posteriorly as anteriorly with an armature of well-marked blunt teeth. *Terminalia*: coxite (0.35 mm.) about twice as long as style (0.15 mm.) which bears four terminal spines and small ventral seta at 0.8; paramere (0.24 mm.) blunt, penis sheath (0.10–0.11 mm) conical with blunt tip; lateral lobe (0.27–0.29 mm.) markedly longer than paramere.

Distribution: ASHANTI, GOLD COAST, BELGIAN CONGO, A.-E. SUDAN, DAHOMEY.

Phlebotomus (Sergentomyia) schwetzi Adler, Theodor & Parrot.

P. schwetzi Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18 : 72.

P. symesi Sinton, 1930, *Indian J. med. Res.* 18 : 175.

P. schwetzi var. *aethiopicus* Parrot, 1936, *Arch. Inst. Pasteur Algér.* 14 : 30.

The description below has been compiled from published descriptions of 217 females and 80 males from the Belgian Congo, Dire Dawa and Mombasa. Types and co-types are in the Hebrew University, Jerusalem, and the Institut Pasteur d'Algérie.

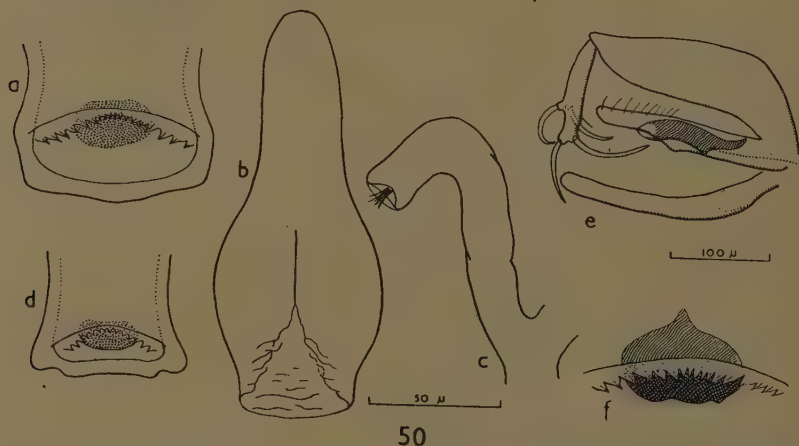


FIG. 50.—*P. schwetzi*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. *P. schwetzi* var. *nigricans*, ♀: f, buccal cavity. (a–e after Adler, Theodor and Parrot, 1929; f after Parrot, 1948.)

♀. Length: 1.5–2.54 mm., hind leg 2.6–3.1 mm. *Antenna*: formula 2/III–XV, segment III (0.155–0.189 mm.) > IV + V, AIII/E = 0.77–0.85, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,(4,3),5, relative lengths 1, 2.5, 3.9, 3.7, 7.7. *Epipharynx*: length 0.20–0.23 mm. *Buccal cavity*: with about 16–18 pointed teeth on an arc concave posteriorly, the median teeth being narrower and straighter than the lateral ones; pigmented plate elliptical. *Pharynx*: more than twice as wide posteriorly as anteriorly, armed with fine transverse wavy ridges without any pointed teeth. *Wing*: length 1.4–1.8 mm., width 0.5–0.55 mm., alar index 0.5–1.2, delta + 0.05 to 0.18. *Spermatheca*: simple, tubular, of *minutus* type.

♂. Length: 1.5–2.7 mm., hind leg 2.5–3 mm. *Antenna*: formula 1/III–XV, segment III (0.2 mm.) < or = IV + V, AIII/E = 0.98–1.1, ascoid on IV = 0.3 length of segment.

Palp: formula 1,2,4,3,5, relative lengths 1, 2.3, 3.6, 3.1, 7.4. *Buccal cavity*: with about 16 pointed teeth on an arc concave posteriorly; pigmented plate elliptical, sometimes absent. *Pharynx*: twice as wide posteriorly as anteriorly, armed as in the female with transverse ridges but no teeth. *Wing*: length 1.4–1.77 mm., width 0.28–0.40 mm., alar index 0.5–0.77, delta + 0.03 to 0.07 mm. *Terminalia*: coxite (0.23–0.32 mm.) nearly 2.5 times as long as style (0.1–0.12 mm.), which bears two terminal spines and two sub-terminal or submedian ones on a prominent apophysis of variable size; small ventral seta level with subterminal spines or between the two pairs; paramere with rounded tip, penis sheath 4–5 times as long as wide, finger-shaped, curved and blunt, with a dorsal notch near the tip; lateral lobe (0.25 mm.) longer than paramere.

Distribution: A.-E. SUDAN, TRANSVAAL, KENYA, ABYSSINIA, SENEGAL, FRENCH GUINEA, BELGIAN CONGO, widely distributed in EQUATORIAL AFRICA.

Phlebotomus (Sergentomyia) schwetzi var. *nigricans* Parrot.

P. schwetzi var. *nigricans* Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26: 269.

Type specimen in the British Museum. The description below is after Parrot, from three females from Katire, A.-E. Sudan.

♀. *Length*: 2.5 mm., hind leg 3.64 mm. *Antenna*: formula 2/III–XV, segment III (0.25–0.28 mm.) > IV + V, AIII/E = 1.1, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.9, 5.3, 6.3, 12.5. *Epipharynx*: length 0.23–0.24 mm. *Buccal cavity*: with 17 pointed teeth almost on a straight line, the median ones being straighter than the lateral ones; pigmented plate very dark, roughly elliptical with a short anterior prolongation. *Pharynx*: as in *P. schwetzi*. *Wing*: length 2.24 mm., width 0.6 mm., alar index 1.1, delta + 0.1 mm. *Spermatheca*: tubular, of *minutus* type ♂. Unknown.

The female of this variety is separated from typical *P. schwetzi* by the heavily pigmented buccal area, the greater length of AIII (AIII/E = 1.1 as compared with 0.7–0.85) and by the palpal formula, segment 4 being longer than segment 3 by about 30 μ .

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) guiraudi Kervran.

P. guiraudi Kervran, 1946, *Ann. Parasit. hum. comp.* 21: 155.

Type locality Bamako (Koulouba), French Sudan. This species is known from one female only and is obviously closely related to *P. schwetzi*. The description below is after Kervran.

♀. *Length*: 1.9 mm. *Antenna*: segment III (0.2 mm.) < IV + V, AIII/E = 0.8, ascoids on IV = 0.5 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.5, 3.8, 3.5, 8.2. *Epipharynx*: length 0.25 mm. *Buccal cavity*: with 16 broad teeth increasing in length from the centre to the periphery; pigmented plate oval with long axis lying transversely. *Pharynx*: about twice as wide posteriorly as anteriorly, with fine scale-like folds in its posterior part. *Wing*: length 1.75 mm., width 0.45 mm., alar index 1, delta + 0.2 mm. *Spermatheca*: of *minutus* type.

Distribution: FRENCH SUDAN.

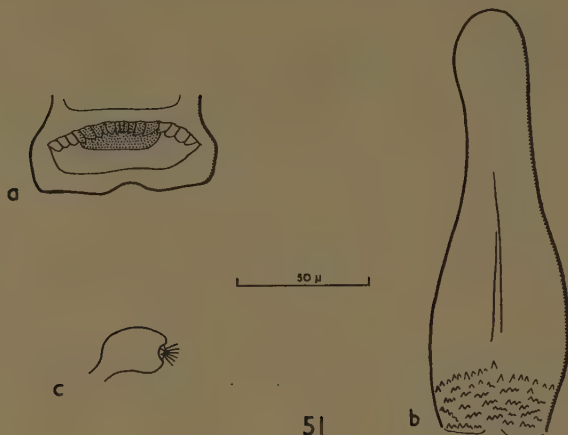


FIG. 51.—*P. guiraudi*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. (After Kervran, 1946)

Phlebotomus (Sergentomyia) freetownensis Sinton.

P. freetownensis Sinton, 1930, *Indian J. med. Res.* 18 : 171.

This species is known from one female only, from Sierra Leone. In this work the name *africanus* is regarded as a synonym of *P. squamipleuris* (see p. 408) and *P. freetownensis* becomes the typical example of the various forms previously known as *P. africanus* and its varieties. The description below is after Sinton.

♀. Length : 2.7 mm. Antenna : formula 2/III-XV, segment III (0.192 mm.) = IV + V, AIII/E = 1.2, ascoid on IV = 0.25 length of segment. Palp : formula 1,2,3,4,5, relative lengths 1, 2.8, 4.4, 4.9, 10. Epipharynx : length 0.165 mm. Buccal cavity : with about 60 narrow parallel teeth on an arc concave posteriorly; pigmented plate triradiate with thickened lateral arms, which show rounded ends while the median or anterior one is pointed and the posterior margin is concave posteriorly. Pharynx : flask-shaped, about 2.5 times as wide posteriorly as anteriorly, armed with numerous backwardly directed spines, of which there are about 20 in a transverse row at the widest part of the organ. Wing : length 1.857 mm., width 0.5 mm., alar index 1.06, delta + 0.193 mm. Spermatheca : an elongated oval capsule twice as long as wide, ending in a narrow duct.

♂. Unknown.

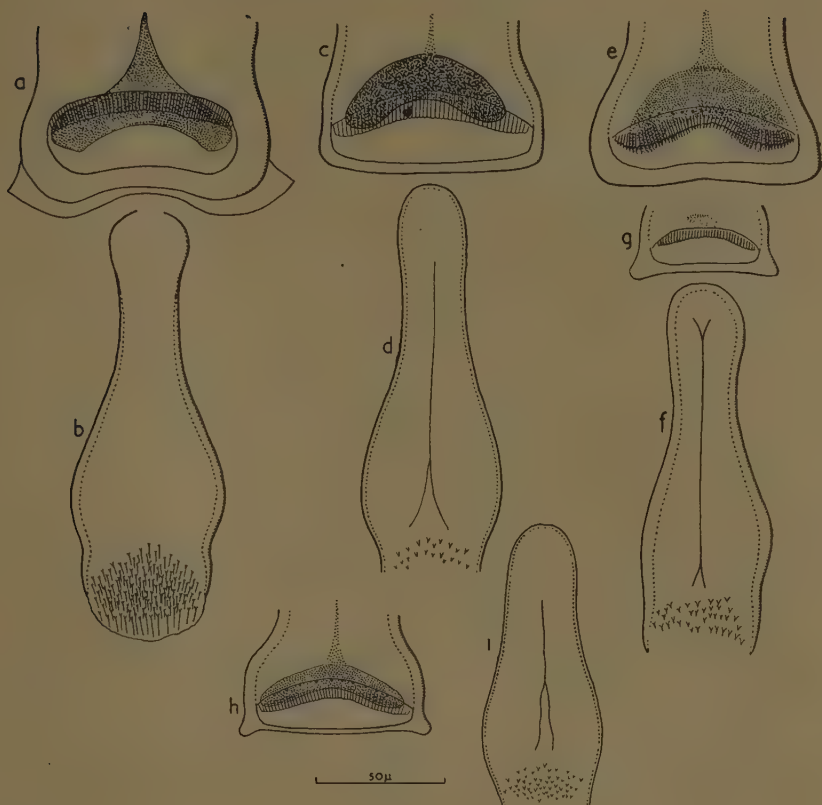
Distribution : SIERRA LEONE.

Phlebotomus (Sergentomyia) freetownensis var. *magnus* Sinton.

P. africanus Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18 : 72.

P. africanus var. *magnus* Sinton, 1932, *Indian J. med. Res.* 20 : 565.

P. africanus var. *magnus* was described by Sinton from one female only. Theodor (1948) considered that this was possibly only a large specimen of *P. africanus* and it agrees closely with the form of that species described by Adler Theodor and Parrot from the Belgian Congo. In this work the Ethiopian form previously known as *P. africanus* Newstead is included under the name *P.*



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FIG. 52.—*P. freetownensis*, ♀: a, buccal cavity; b, pharynx. *P. f. var. ater*, ♀: c, buccal cavity; d, pharynx. *P. f. var. eremitis*, ♀: e, buccal cavity; f, pharynx. ♂: g, buccal cavity. *P. f. var. longior*, ♀: h, buccal cavity; i, pharynx. (a and b after Sinton, 1930; c, d, h and i after Parrot, 1936; e, f and g after Parrot and De Jolinière, 1945.)

freetownensis var. *magnus*. Type locality Letsitelle, Transvaal. The description below is from published descriptions of 152 females and 180 males from the Belgian Congo and Transvaal.

♀. Length: 1.45–2.45 mm., hind leg 2.3–2.6 mm. Antenna: formula 2/III–XV, segment III (0.135–0.171 mm.) < IV + V, AIII/E = 0.8–1, ascoids on IV = 0.25 length of segment. Palp: formula 1,2,3,4,5, relative lengths 1, 2.2, 3.6, 4.2, 8.1. Epipharynx: length 0.15–0.17 mm. Buccal cavity: with 40–50 straight parallel teeth arranged in a palisade on an arc concave posteriorly; there may be some very small punctiform denticles at the bases of the teeth; pigmented plate sausage-shaped, concave posteriorly and with a paler, triangular, pointed, forward extension. Pharynx: about twice as wide posteriorly as anteriorly, armed with short backwardly directed spines in its posterior part. Wing:

length 1.4–1.77 mm., width 0.36–0.485 mm., alar index 0.52–0.89, delta + 0.04 to 0.14. *Spermatheca* : an elongated oval capsule, opening into a relatively narrow duct.

♂. *Length* : 1.4–2 mm., hind leg 2.1–2.4 mm. *Antenna* : formula 1/III–XV, segment III (0.15–0.19 mm.) < IV + V, AIII/E = 1.1–1.2, ascoids on IV = 0.22 length of segment. *Palp* : formula 1,2,3,4,5, relative lengths 1, 2.3, 3.9, 4.7, 8.5. *Epipharynx* : length 0.132–0.158 mm. *Buccal cavity* : with about 20–30 straight parallel teeth ; no pigmented area. *Pharynx* : about twice as wide posteriorly as anteriorly, armed with short spines as in the female, but fewer and less well developed. *Wing* : length 1.3–1.56 mm., width 0.28–0.41 mm., alar index 0.36–0.84, delta 0 to + 0.09 mm. *Terminalia* : coxite (0.21–0.25 mm.) about twice length of style (0.09–0.11 mm.) which bears four spines, two terminal and two subterminal, with small ventral seta at 0.5 ; paramere 0.14–0.18 mm., penis sheath (0.09–0.10 mm.) conical ending in a sharp point ; lateral lobe 0.18–0.22 mm., longer than paramere.

Distribution : Widely distributed throughout AFRICA.

Phlebotomus (Sergentomyia) freetownensis var. *ater* Parrot.

P. africanus var. *ater* Parrot, 1936, *Arch. Inst. Pasteur Algér.* 14 : 43.

Type specimens in Institut Pasteur d'Algérie. The description below is after Parrot, from three females from Dire Dawa, Abyssinia.

♀. *Length* : 1.86–1.89 mm., hind leg 2.1–2.3 mm. *Antenna* : formula 2/III–XV, segment III (0.13–0.14 mm.) < IV + V, AIII/E = 0.82–0.95. *Palp* : formula 1,2,(3,4),5, relative lengths 1, 1.5, 3.3, 3.3, 5.7. *Epipharynx* : length 0.14–0.15 mm. *Buccal cavity* : 46–48 straight long parallel teeth arranged in a palisade on an arc slightly concave posteriorly ; pigmented plate black, not occupying whole width of buccal cavity and with a small triangular anterior prolongation. *Pharynx* : twice as wide posteriorly as anteriorly, constricted posteriorly and armed with a score of moderately long denticles. *Wing* : length 1.86–1.89 mm., width 0.38–0.42 mm., alar index 0.58–0.66, delta + 0.38–0.42 mm. *Spermatheca* : as in *P. freetownensis*.

♂. Unknown.

This form differs from the other varieties of *P. freetownensis* especially in the form and colour of the pigmented plate, the pharyngeal armature and the relative shortness of the fourth palpal segment.

Distribution : ABYSSINIA.

Phlebotomus (Sergentomyia) freetownensis var. *eremitis* Parrot & de Jolivière.

P. eremitis Parrot & de Jolivière, 1945, *Arch. Inst. Pasteur Algér.* 23 : 56.

P. africanus var. *eremitis* Theodor, 1948, *Bull. ent. Res.* 39 : 85.

The description below is after Parrot and de Jolivière, from 24 males and 10 females from Amgel and Tamanrasset ; type specimens in the Institut Pasteur d'Algérie.

♀. *Length* : 2.2–2.15 mm., hind leg 2.3–2.6 mm. *Antenna* : formula 2/III–XV, segment III (0.114–0.147 mm.) < IV + V, AIII/E = 0.79–0.96, ascoids on IV = 0.3 length of segment, but the ascoids on each segment especially the terminal ones, are unequal in size. *Palp* : formula 1, 2,(3,4), 5, relative lengths 1, 2.5, 4.2, 4.3, 8.5. *Epipharynx* : length 0.13–0.156 mm. *Buccal cavity* : with 60–65 teeth, parallel, straight and long, the extreme lateral ones slightly bigger than the median ones, arranged in a palisade on an arc slightly concave posteriorly ; at the bases of these teeth is a row of about a dozen punctiform denticles ; pigmented plate dark brown, not occupying whole width of buccal cavity, in the form of a crescent slightly concave posteriorly, with irregular posterior margin and a paler anterior triangular prolongation. *Pharynx* : posterior width slightly less than

twice anterior width armed in posterior part with about 40 well-developed, pointed spines. *Wing*: length 1.65–1.79 mm., width 0.31–0.41 mm., alar index 0.47–0.65, delta — 0.017 to + 0.051 mm. *Spermatheca*: as in *P. freetownensis*.

♂. *Length*: 1.82–2.05 mm., hind leg 1.9–2.4 mm. *Antenna*: formula 1/III–XV, segment III (0.13–0.16 mm.) < IV + V, AIII/E = 0.92–1.06, ascoids on IV = 0.2 length of segment. *Palp*: formula 1, 2, (3,4), 5, relative lengths 1, 2.3, 4.1, 4.1, 7.8. *Epipharynx*: length 0.13–0.16 mm. *Buccal cavity*: with 30–35 long parallel monomorphic teeth in a palisade on an arc slightly concave posteriorly; anteriorly a row of 8–10 punctiform denticles, sometimes not visible; pigmented area dark brown, small, sometimes absent. *Pharynx*: posterior width about twice anterior width armed with transverse folds bearing a few short spines. *Wing*: length 1.3–1.7 mm., width 0.27–0.36 mm., alar index 0.4–0.58, delta + 0.085 to + 0.017 mm. *Terminalia*: coxite (0.22–0.25 mm.) twice as long as style (0.09–0.11 mm.) which bears two terminal and two subterminal spines and small ventral seta at 0.6; paramere (0.16–0.17 mm.) rounded, penis sheath (0.09–0.10 mm.) tapering to a fine point; lateral lobe 0.195–0.21 mm.

The female is distinguished from other varieties of *P. freetownensis* by the number of the buccal teeth and from var. *niger* by the pigmented plate. For the differentiation of the male see p. 477 (var. *niger*).

Distribution: AL AHAGGAR, A.-E. SUDAN.

Phlebotomus (Sergentomyia) freetownensis var. *longior* Parrot.

P. africanus var. *longior* Parrot, 1936, Arch. Inst. Pasteur Algér. 14: 40.

The description below is after Parrot, from two females and three males from Dire Dawa, Abyssinia. Type specimens in the Institut Pasteur d'Algérie.

♀. *Length*: 2.1–2.2 mm., hind leg 2.4–2.8 mm. *Antenna*: formula 2/III–XV, segment III (0.14–0.18 mm.) < IV + V, AIII/E = 0.84–0.87. *Palp*: formula 1, 2, 3, 4, 5, relative lengths 1, 2.4, 3.7, 4.2, 6.2. *Epipharynx*: length 0.17–0.19 mm. *Buccal cavity*: 48–50 parallel narrow teeth arranged in a palisade on an arc slightly concave posteriorly; 10–12 anterior slightly pointed denticles; pigmented area brown, covering the whole width of the buccal cavity and prolonged anteriorly by a clear triangular extension. *Pharynx*: a little less than twice as wide posteriorly as anteriorly, slightly constricted posteriorly and bearing rather numerous short pointed teeth. *Wing*: length 1.6–1.9 mm., width 0.4 mm., alar index 0.6–0.8, delta + 0.05 to + 0.07 mm. *Spermatheca*: as in *P. freetownensis*.

♂. *Length*: 1.9–2.3 mm., hind leg 2.1–2.6 mm. *Antenna*: formula 1/III–XV, segment III (0.14–0.21 mm.) < IV + V, AIII/E = 1.07–1.18. *Palp*: formula 1, 2, 3, 4, 5, relative lengths 1, 2.3, 3.8, 4, 4.6. *Buccal cavity and pharynx*: as in *P. freetownensis* var. *magnus*. *Wing*: length 1.7–1.8 mm., width 0.31 mm., alar index 0.5–0.6, delta + 0.02 to + 0.04 mm. *Terminalia*: in general as in *P. freetownensis* var. *magnus*, but the penis sheath (0.10–0.13 mm.) in the form of an elongated cone with a delicate slightly curved point.

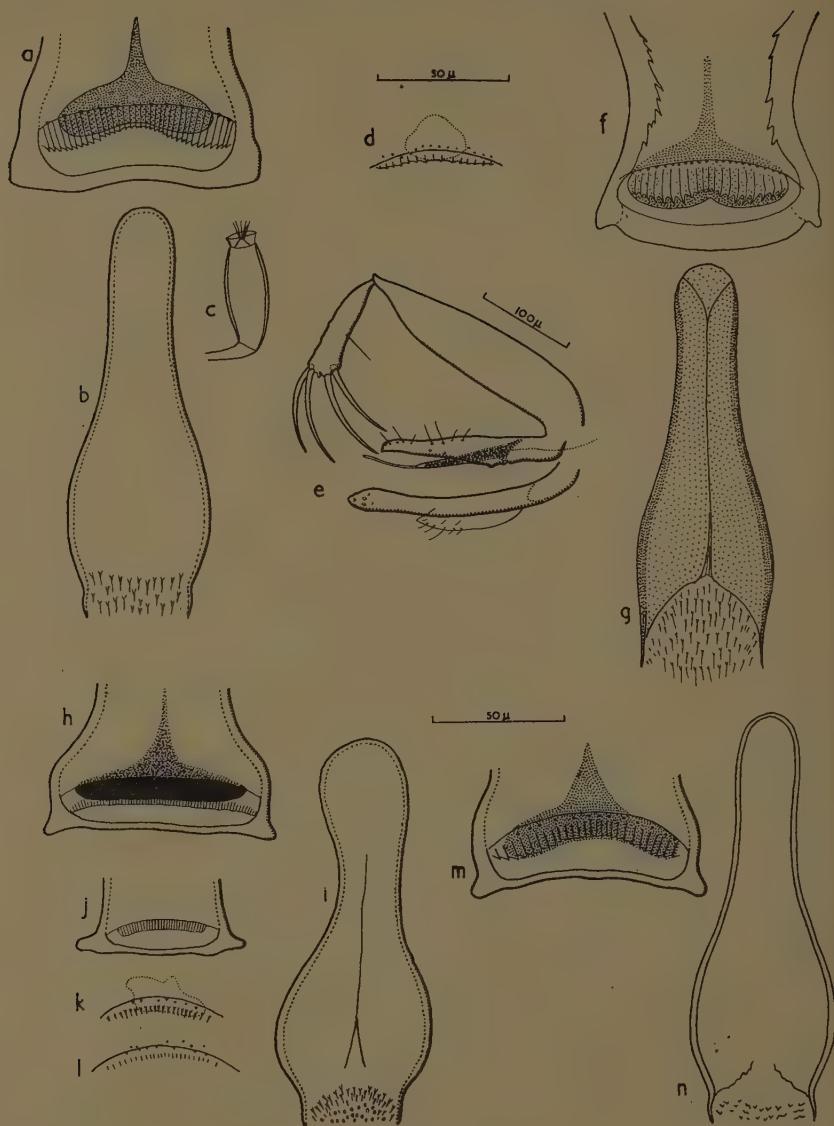
This form is differentiated from other varieties of *P. freetownensis* by the much greater length of the penis in the male and by the number of buccal teeth and the number and length of the pharyngeal teeth.

Distribution: ABYSSINIA.

Phlebotomus (Sergentomyia) freetownensis var. *meridianus* De Meillon & Lavoipierre.

P. africanus var. *meridianus* De Meillon & Lavoipierre, 1944, J. ent. Soc. S. Afr. 7: 38.

The description below is after De Meillon and Lavoipierre from two females from Onderstepoort, Transvaal. Type specimen in the South African Institute for Medical Research, Johannesburg.



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FIG. 53.—*P. freetownensis* var. *magnus*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. *P. f.* var. *meridionalis*, ♀: *f*, buccal cavity; *g*, pharynx. *P. f.* var. *niger* ♀: *h*, buccal cavity; *i*, pharynx. ♂: *j-l*, buccal cavity. *P. f.* var. *sudanicus*. ♀: *m*, buccal cavity; *n*, pharynx. (*a-c* after Theodor, 1948; *d, k* and *l* after Parrot, 1948; *e* after Adler, Theodor and Parrot, 1929; *f* and *g* after De Meillon and Lavoipierre, 1944; *h-j* after Parrot and Schwetz, 1937; *m* after Parrot, Mornet and Cadenat, 1945; *n* after Theodor, 1933.)

♀. *Length* : 2.72 mm., hind leg 2.64 mm. *Antenna* : formula 2/III-XV, segment III (0.16 mm.) < IV + V, AIII/E = 0.9, ascoid on IV = 0.25 length of segment. *Palp* : formula 1,2,(3,4),5, relative lengths 1, 1.9, 4.3, 4.3, 8.8. *Buccal cavity* : with about 20 large pointed teeth with their bases nearly in a straight line, about three median and one or two of the extreme lateral teeth shorter than the rest ; immediately anterior to this row of teeth a row of fine punctiform teeth ; pigmented plate large, mushroom-shaped. *Pharynx* : posterior width about twice anterior width, armed with numerous sharply pointed teeth posteriorly. *Wing* : length 1.9 mm., width 0.54 mm., alar index 0.74, delta + 0.1 mm. *Spermathecae* : elliptical capsules as in *P. freetownensis*.

♂. Unknown.

This form differs from all other varieties of *P. freetownensis* in the small number of buccal teeth.

Distribution : TRANSVAAL.

Phlebotomus (Sergentomyia) freetownensis var. *niger* Parrot & Schwetz.

P. africanus var. *niger* Parrot & Schwetz, 1937, *Rev. Zool. Bot. afr.* 29 : 221.

P. africanus var. *niger* Theodor, 1933, *Bull. ent. Res.* 24 : 166.

The description below is from the original description of 17 females and 15 males from several places in the Belgian Congo (types in the Museum of the Belgian Congo, Tervueren) and from Theodor (1933).

♀. *Length* : lengths of body, hind leg, antenna and its parts, palp, wing and spermatheca as in *P. freetownensis* var. *magnus* from the Belgian Congo. *Buccal cavity* : with 60-70 uniform parallel teeth in a palisade on an arc slightly concave posteriorly, and no anterior denticles ; pigmented plate black and sausage-shaped, occupying nearly the whole width of the cavity, with an anterior subtriangular pale prolongation. *Pharynx* : with posterior width twice anterior width, strongly constricted posteriorly, and bearing about 60 fairly long-pointed denticles, smaller, stronger, and more numerous than in *P. freetownensis* var. *magnus*.

♂. *Length* : measurements of body length, hind leg, palp, antenna and wing as in *P. freetownensis* var. *magnus* from the Belgian Congo. *Buccal cavity* : with 28-36 uniform straight parallel teeth, pigmented plate absent. *Pharynx* : as in var. *magnus*, but generally a little wider.

The female of this variety differs from other varieties of *P. freetownensis* by the very dark colour of the buccal pigmented plate (this character makes it easily recognisable) also by the large number of buccal teeth and the character of the pharyngeal armature. The male is distinguished by the greater number of buccal teeth from all other known varieties except var. *eremitis* from which it can be distinguished by the palpal formula and the position of the small ventral seta (at 0.75 in *niger* and 0.6 in *eremitis*).

Distribution : A.-E. SUDAN, BELGIAN CONGO, NIGERIA, FRENCH SUDAN, FRENCH CONGO, FRENCH GUINEA, DAHOMEY, IVORY COAST, UGANDA.

Phlebotomus (Sergentomyia) freetownensis var. *sudanicus* Theodor.

P. africanus var. *sudanicus* Theodor, 1933, *Bull. ent. Res.* 24 : 541.

The description below is from five males and five females from the Anglo-Egyptian Sudan.

♀. *Length* : 1.4-2.0 mm., hind leg 2.1-2.7 mm. *Antenna* : formula 2/III-XV, segment III (0.11-0.16 mm.) < IV + V, AIII/E = 0.9, ascoids on IV = 0.3 length of segment. *Palp* : formula 1,2,3,4,5, relative lengths 1, 2.2, 3.6, 4.0, 7.2. *Epipharynx* : length 0.11-0.17 mm. *Buccal cavity* : with 30-33 teeth and a small point-like denticle at the base of

every second tooth in the armature. *Pharynx*: as in *P. freetownensis* var. *magnus*, but the teeth are much smaller, sometimes appearing as rows of points. *Wing*: length 1.3–1.9 mm., width 0.3–0.4 mm., alar index 0.5–0.7, delta + 0.03 to + 0.1 mm. *Spermatheca*: as in *P. freetownensis*.

♂. *Length*: 1.8–2.3 mm., hind leg 1.9–3.0 mm. *Antenna*: formula 1/III–XV, segment III (0.16–0.20 mm.) < or = IV + V, AIII/E = 1–1.1, ascoid on IV = 0.2 length of segment. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 2, 4, 5, 6.7. *Epipharynx*: length 0.14–0.15 mm. *Buccal cavity*: with about 16 equal teeth on an arc slightly concave posteriorly, pigmented area absent. *Pharynx*: about twice as wide posteriorly as anteriorly armed with transverse ridges bearing delicate teeth. *Wing*: length 1.1–1.45 mm., width 0.2–0.28 mm., alar index 0.33–0.4, delta + 0.01 to + 0.03 mm. *Terminalia*: coxite (0.21–0.26 mm.) about 2.5 times as long as style, which bears four terminal spines, and small ventral seta at 0.8; paramere (0.15–0.20 mm.) shorter than lateral lobe (0.20–0.23 mm.); penis sheath (0.05–0.10 mm.) conical, tapering to a sharp point.

Distribution: A.-E. SUDAN, FRENCH WEST AFRICA, KENYA.

Phlebotomus (Sergentomyia) babu Annandale.

P. babu Annandale, 1910, *Rec. Indian Mus.* 4: 49.

P. babu Sinton, 1928, *Indian J. med. Res.* 16: 297; 1932, *ibid.* 20: 55; 1933, *ibid.* 21: 417.

The following description is from the papers of Sinton and the examination of five females and 16 males in the British Museum from India, Ceylon and Mauritius.

♀. *Length*: 1.5–2.1 mm., hind leg 2.4–2.7 mm. *Antenna*: formula 2/III–XV, segment III (0.10–0.14 mm.) = IV + V, AIII/E = 0.9–1.0, ascoids on IV = 0.4 length of segment.

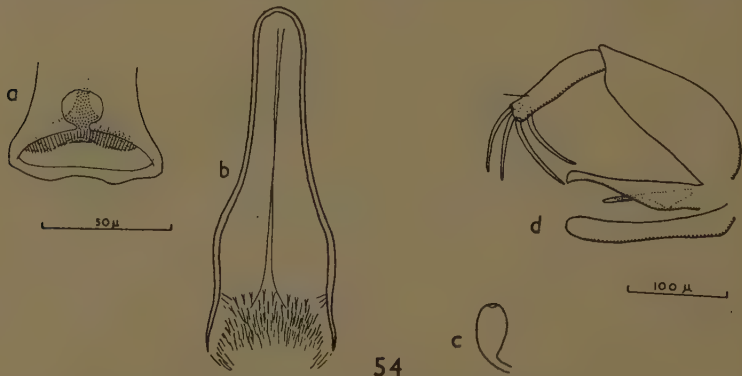


FIG. 54.—*P. babu*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, terminalia. (From specimens from Mauritius.)

Palp: formula 1,2,(3,4),5, relative lengths 1, 2.5, 3.5, 3.5, 7.2. *Epipharynx*: length 0.13–0.15 mm. *Buccal cavity*: with 36–40 equal pointed teeth on a row concave posteriorly and a row of anterior small punctiform denticles anteriorly to which the buccal plate shows a festooned edge with a well-marked median anterior notch; pigmented area in the shape of a very wide triangle with apex directed anteriorly and base not extending across whole width of buccal cavity. *Pharynx*: slightly more than twice as wide posteriorly as anteriorly, constricted in its wide posterior portion, which is armed with scale-like teeth having

long, backwardly directed points; in the posterior part of the armature only these long filiform points are seen. *Wing*: length 1.4–1.6 mm., width 0.34–0.42 mm., alar index 0.5–0.62, delta +0.05 to +0.1 mm. *Spermatheca*: thin-walled elliptical capsules with narrow ducts.

♂. *Length*: 1.6–1.8 mm., hind leg 2.1–2.4 mm. *Antenna*: formula 1/III–XV, segment III (0.12–0.13 mm.) > IV + V, AIII/E = 0.6–1, ascoid on IV = 0.2 length of segment. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 2, 3.6, 3.6, 7.5. *Epipharynx*: length 0.14–0.17 mm. *Buccal cavity*: with two rows of poorly developed denticles, variable and rather difficult to count, approximately 17 in each row; pigmented area very small and centrally situated. *Pharynx*: twice as wide posteriorly as anteriorly, armed with irregular faint wavy transverse rows of delicate pointed teeth. *Wing*: length 1.27–1.53 mm., width 0.34 mm., alar index 0.25–0.6, delta +0.03 to –0.08 mm. *Terminalia*: coxite (0.18–0.21 mm.) slightly more than twice as long as style (0.15 mm.), which bears four terminal spines and small ventral seta at 0.7; paramere 0.14 mm., penis sheath (0.06 mm.) narrow, straight, with blunt tip, lateral lobe (0.16 mm.) slightly longer than paramere.

Distribution: MAURITIUS; occurs also in the ORIENTAL REGION.

Phlebotomus (Sergentomyia) crosarai Parrot and Wanson.

P. crosarai Parrot & Wanson, 1946, *Rev. Zool. Bot. afr.* 39: 225.

Type specimens in the Museum of the Belgian Congo at Tervueren. The descriptions below are after Parrot and Wanson's original descriptions of 14 females from Bongolokoro and Luna, Belgian Congo.

The female is distinguished from other members of the subgenus by its antennal formula.

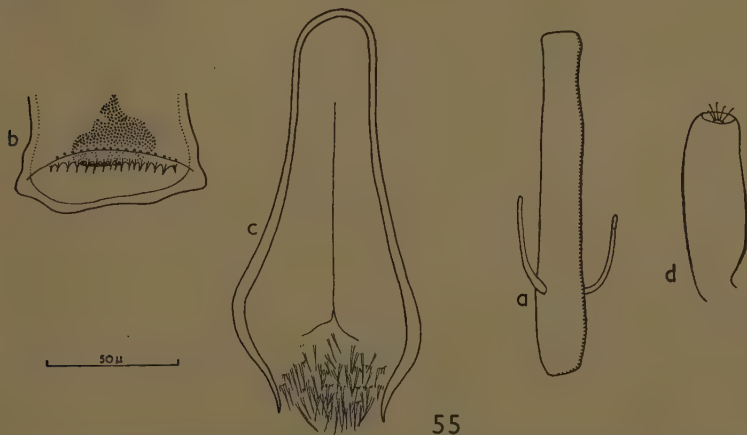


FIG. 55.—*P. crosarai*, ♀: a, fourth antennal segment; b, buccal cavity; c, pharynx; d, spermatheca. (After Parrot and Wanson, 1936.)

♂. *Length*: 2.12–2.34 mm. *Antenna*: formula 2/V–XIII, 1/XIV–XV, segment III (0.27–0.28 mm.) > IV + V, AIII/E = 1.4–1.6, ascoids relatively short and fragile, those on V = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.2, 4.5, 5.5, 8. *Epipharynx*: length 0.17–0.2 mm. *Buccal cavity*: with a row slightly concave posteriorly, of 18–20 equal pointed teeth; anterior to these one or two or sometimes three rows of denticles, the first of 18–20 appearing as large dots, the second of 8–10 delicate denticles and the third

of 1-4 also delicate; pigmented area brown, irregularly triangular with a more or less marked slightly paler forward process. *Pharynx*: about twice as wide posteriorly as anteriorly, armed with about 50 long strong spines with thread-like tips. *Wing*: 1.87-2.34 mm. long, 0.58-0.84 mm. wide, alar index 1.6-3.5, delta + 0.4 to + 0.5 mm., transverse veins a little nearer the base of the wing than in other species. *Spermatheca*: an elongated capsule.

♂. Unknown.

Distribution: BELGIAN CONGO.

Phlebotomus (Sergentomyia) yvonnae Parrot and Schwetz.

P. yvonnae Parrot & Schwetz, 1937, *Rev. Zool. Bot. afr.* 29: 221.

This species is known from one female only, from Siboma, Belgian Congo, and the type specimen is in the Museum of the Belgian Congo at Tervueren. The description below is after Parrot and Schwetz.

♀. *Length*: 1.88 mm. *Antenna*: formula 2/III-XV, segment III (0.18 mm.) < IV + V, AIII/E = 0.94, ascoids short, that on IV = 0.3 length of segment. *Palp*: formula

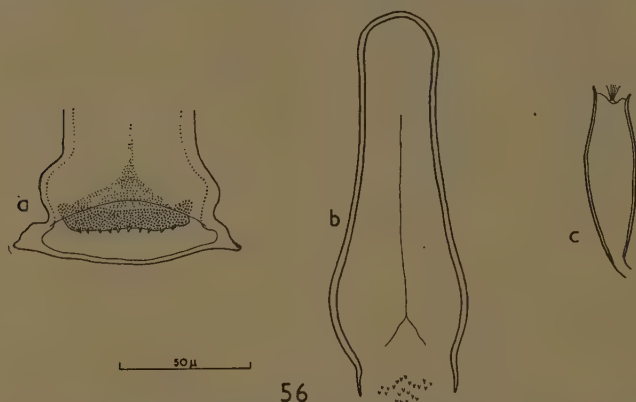


FIG. 56.—*P. yvonnae*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. (After Parrot and Schwetz, 1937.)

1,2,3,4,5, relative lengths 1, 2.4, 3.8, 4.2, 5. *Epipharynx*: length 0.19 mm. *Buccal cavity*: with 10 strong pointed teeth, pigmented area light brown, shaped like an irregular trapezium with its base anteriorly, covering nearly the whole width of the buccal cavity and with a subtriangular paler anterior extension. *Pharynx*: with posterior width a little less than anterior width, sharply constricted towards the posterior end which bears about 30 short pointed denticles. *Wing*: length 1.67 mm., breadth 0.43 mm., alar index 0.77, delta + 0.11 mm. *Spermatheca*: an oblong capsule like that of *P. freetownensis*, but longer.

♂. Unknown.

Distribution: BELGIAN CONGO.

Phlebotomus (Sergentomyia) ingrami Newstead.

P. ingrami Newstead, 1914, *Bull. ent. Res.* 5: 179.

P. ingrami Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18: 72.

P. ingrami Bequaert & Walravens, 1930, *ibid.* 19: 34.

P. raptus Parrot, Mornet & Cadenat, 1945, *Arch. Inst. Pasteur Algér.* 23 : 281.

P. ingrami Parrot, 1948, *ibid.* 26 : 121.

Type specimens in the British Museum. The description below is after Parrot (1948), who reviews previous records.

♀. Length : 2.23 mm., hind leg 3.2 mm. Antenna : formula 2/III-XV, segment III (0.22-0.25 mm.) > IV + V, AIII/E = 1.1-1.4, ascoids on IV = 0.3 length of segment. Palp : formula 1,2,3,4,5, relative lengths 1, 2.4, 4.2, 5.2, 9. Epipharynx : length 0.16-0.20 mm. Buccal cavity : with 24-28 pointed teeth on an arc slightly concave posteriorly, the median teeth being more or less prominent ; one, two or three rows of anterior small denticles, the middle row consisting of 7-10 stout and pigmented denticles ; pigmented plate not extending across whole width of buccal cavity, rounded anteriorly, with a median notch in its posterior border. Pharynx : 1.5 times as wide posteriorly as anteriorly, with several rows of fine ridges bearing very small spines. Wing : length 2.0-2.17 mm., width

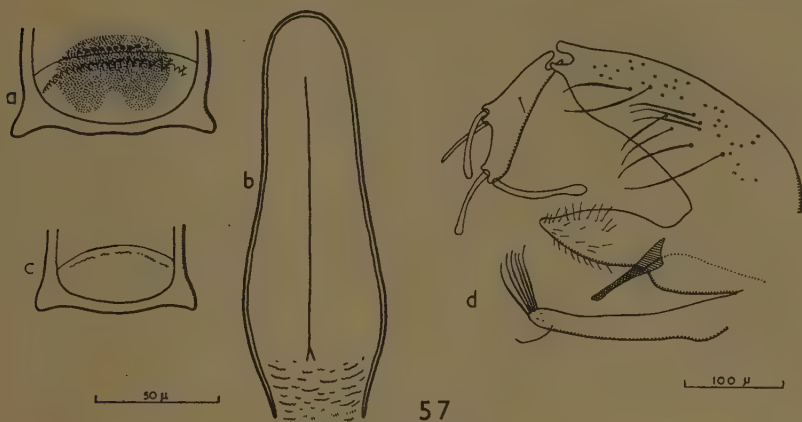


FIG. 57.—*P. ingrami*, ♀: a, buccal cavity ; b, pharynx ; ♂: c, buccal cavity ; d terminalia. (After Parrot, 1948.)

0.53-0.55 mm., alar index 1-1.3, delta + 0.19 to 0.25 mm. Spermatheca : simple, tubular, of *minutus* type.

♂. Length : 1.85-2.04 mm., hind leg 3.1 mm. Antenna : formula 1/III-XV, segment III (0.20-0.24 mm.) > IV + V, AIII/E = 1.5-1.6, ascoid on IV = 0.25 length of segment. Palp : formula 1,2,3,4,5, relative lengths 1, 2.5, 4.3, 5.8, 9.3. Epipharynx : length 0.126-0.15 mm. Buccal cavity : with 22-30 small short pointed teeth, often not clearly visible, on an arc slightly concave posteriorly ; pigmented plate absent. Pharynx : About 1.5 times as wide posteriorly as anteriorly armed with fine folds bearing small spines. Wing : length 1.65-1.84 mm., width 0.41-0.46 mm., alar index 0.83-0.90, delta + 0.085 to 0.12 mm. Terminalia : coxite (0.25-0.3 mm.) about 2.5 times as long as style (0.09-0.13 mm.), which bears four strong spatulate spines, two of which are terminal and two central or nearly central, with small ventral seta at 0.3 ; paramere lance-shaped (0.17-0.20 mm.), penis sheath (0.09-0.11 mm.) conical with a subapical lateral dilatation ; lateral lobe (0.19-0.21 mm.), bearing at its tip 6-8 long hairs slightly recurved.

Distribution : ASHANTI, BELGIAN CONGO, IVORY COAST, GOLD COAST, UGANDA, A.-E. SUDAN.

Phlebotomus (Sergentomyia) serratus Parrot & Malbrant.

P. serratus Parrot & Malbrant, 1945, *Arch. Inst. Pasteur Algér.* 23 : 121.

P. serratus Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond. (B)* 15 : 61.

P. serratus Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26 : 121.

Type specimen from Ouesso, Middle Congo, in the Institut Pasteur d'Algérie. The following description is mainly after Parrot (1948) from the published descriptions of 4 males and two females from the A.-E. Sudan and French Congo.

♀. *Length* : 2.04–2.13 mm., hind leg 2.55–3.0 mm. *Antenna* : formula 2/III–XV, segment III (0.2–0.22 mm.) > IV + V, AIII/E = 1.1–1.4, ascoid on IV = 0.3 length of segment. *Palp* : formula 1,2,3,4,5, relative lengths 1, 2.3, 3.8, 5.5, 8.2. *Epipharynx* : length 0.15–0.17 mm. *Buccal cavity* : with 40–52 pointed monomorphic teeth on an arc

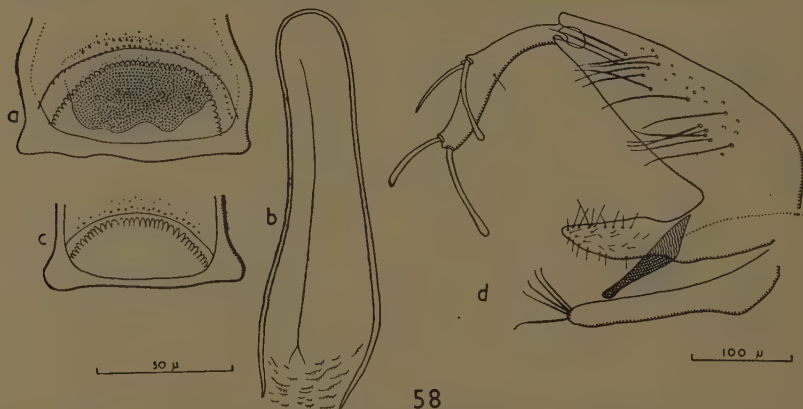


FIG. 58.—*P. serratus*, ♀: *a*, buccal cavity; *b*, pharynx. ♂: *c*, buccal cavity; *d*, terminalia. (*a*, *c* and *d* after Parrot, 1948; *b* after Parrot and Malbrant, 1945.)

strongly concave posteriorly, the 8–10 median teeth sometimes forming a backwardly projecting salient in the middle of the arc; three rows of anterior punctiform denticles, the posterior row being most prominent; pigmented plate not extending across whole width of buccal cavity, rounded anteriorly with a notch in its posterior margin. *Pharynx* : about twice as wide posteriorly as anteriorly, armed with fine ridges bearing small spines. *Wing* : length 1.8–2.13 mm., width 0.44–0.51 mm., alar index 0.85–1.0, delta + 0.15 to 0.19 mm. *Spermatheca* : simple, tubular, of *minutus* type.

♂. *Length* : 2.0–2.4 mm., hind leg 2.8–3.0 mm. *Antenna* : formula 1/III–XV, segment III (0.22–0.27 mm.) > or = IV + V, AIII/E = 1.7–1.8, ascoid on IV = 0.2 length of segment. *Palp* : formula 1, 2, 3, 4, 5, relative lengths 1, 2.7, 4.4, 6, 10. *Epipharynx* : length 0.13–0.16 mm. *Buccal cavity* : with 27–34 straight narrow teeth on an arc strongly concave posteriorly and two irregular rows of anterior punctiform denticles, sometimes occasional members of a third row; pigmented plate absent. *Pharynx* : about 1.5 times as wide posteriorly as anteriorly with faint wavy transverse ridges and very small spines. *Terminalia* : coxite (0.3–0.32 mm.) 1.5 times as long as style (0.15–0.2 mm.) which bears four strong spatulate spines, two of which are terminal and two central or nearly central, with small ventral seta arising near origin of central spines; paramere

(0.2 mm.) lance-shaped; penis sheath (0.10 mm.) conical, with subapical lateral dilatation; lateral lobe (0.2–0.23 mm.) bearing 6–8 long recurved hairs at its free extremity.

Distribution: FRENCH CONGO, A.-E. SUDAN.

Phlebotomus (Sergentomyia) kirki Parrot.

P. kirki Parrot, 1948, *Arch. Inst. Pasteur Algér.* 26: 121.

Type specimens in the British Museum. The description below is after Parrot, from two females and one male from Li Rangu, A.-E. Sudan.

♀. Length: 2.56–2.62 mm., hind leg 3.16 mm. Antenna: formula 2/III–XV, segment III (0.21–0.23 mm.) > IV + V, AIII/E = 1.2–1.4, ascoids on IV = 0.4 length of segment.

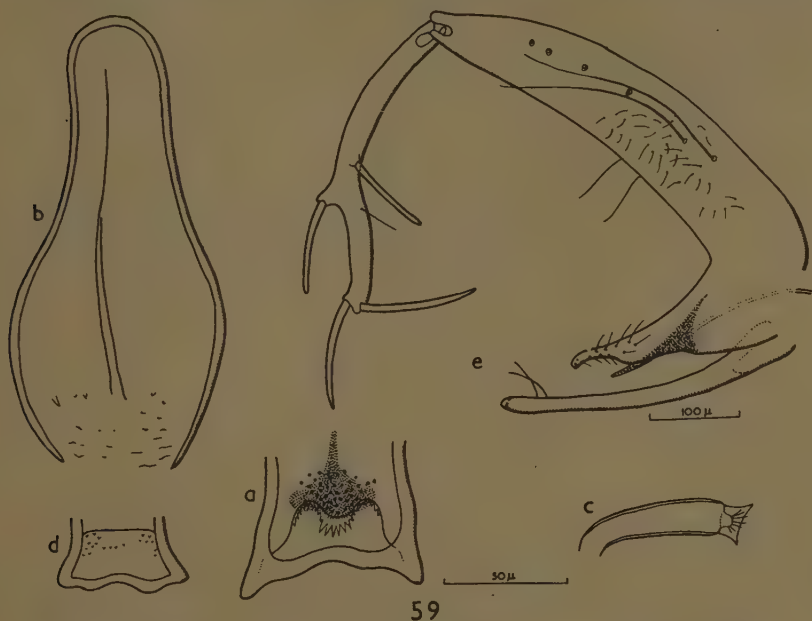


FIG. 59.—*P. kirki*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (After Parrot, 1948.)

Palp: formula 1,2,3,4,5, relative lengths 1, 2.4, 4.3, 4.5, 7. *Epipharynx*: length 0.17 mm. *Buccal cavity*: with 22–24 pointed teeth, the 7–8 median ones larger than the laterals, and projecting strongly backwards, the arrangement of the armature being like a rounded letter M; an anterior patch of denticles; pigmented plate brown, lozenge-shaped, with its axis transverse with a slightly paler anterior triangular narrow extension. *Pharynx*: globular with its posterior width a little more than twice its anterior width, armed posteriorly with some scarcely visible short sinuous folds. *Wing*: length 2–2.1 mm., width 0.44–0.46 mm. (five times as long as broad), alar index 0.78–0.9, delta + 0.153 to 0.20 mm. *Spermatheca*: a long sub-cylindrical tube with rigid walls opening into a wide duct of the same diameter.

♂. *Length*: 2.5 mm. *Antenna*: missing. *Palp*: formula 1,2,3,.. (last two segments missing), relative lengths 1, 2.3, 3.7,. . . *Epipharynx*: length 0.144 mm. *Buccal cavity*: with 21 very short pointed teeth, irregularly arranged in three groups, a median one of four teeth and two lateral groups of 8-9, the median teeth a little stronger than the lateral ones and projecting posteriorly; no pigmented plate visible. *Pharynx*: posterior width about twice anterior width, bearing posteriorly some folds bordered with very fine teeth. *Wing*: lanceolate, very long, about six times as long as broad; length 1.72 mm., width 0.29 mm., alar index 0.47, delta + 0.017. *Terminalia*: coxite (0.45 mm.) 1.5 times length of style, which is 0.31 mm.; inner surface of coxite with numerous short hairs and six flat long strong silky hairs with well-developed bases; style long, nearly ten times as long as wide, with four long spatulate spines, an antero-internal one at the middle of the style, a postero-internal one a little below it, and the two others terminal, with small non-deciduous seta arising near the origin of the submedian spine; paramere (0.22 mm.) turned slightly upward and hooked; penis sheath (0.114 mm.) an elongated cone with blunt tip, slightly turned up; lateral lobe 0.30 mm., unarmed, three-quarters length of coxite.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) notatus Parrot.

P. notatus Parrot, 1938, *Arch. Inst. Pasteur Algér.* 16 : 213.

Type locality Dire Dawa, Abyssinia. This species is known from one female only, and Theodor (1948) points out that the position of the species with reference to *P. sylvestris* Sinton must be reconsidered when the male is described. The description of the female given here is after Parrot.

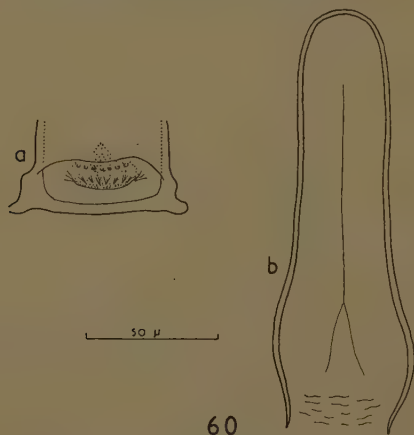


FIG. 60.—*P. notatus*, ♀: a, buccal cavity; b, pharynx. (After Parrot, 1938.)

♀. *Length*: 2.07 mm., hind leg 2.47 mm. *Antenna*: formula 2/III-XV, segment III (0.15 mm.) < IV + V, ascoids short, those on IV = 0.4 length of segment. AIII/E = 0.84. *Palp*: formula 1,2,(4,3),5, relative lengths 1, 2.2, 4, 3.9, 6.4. *Epipharynx*: length 0.178 mm. *Buccal cavity*: with nine pointed teeth, the three median a little shorter than the lateral ones; a row of seven anterior subconical strong denticles resembling those of *P. sylvestris* Sinton, but clearly separated from each other and less numerous; pigmented

plate dark brown and shaped like an irregular crescent, not reaching the sides of the cavity, with a forward prolongation, subtriangular, paler, and rounded at the tip. *Pharynx*: with posterior width 1.5 times anterior width, surrounded posteriorly with fine folds. *Wing*: length 1.61 mm., width 0.32 mm., alar index 0.66, delta + 0.085 mm. *Spermatheca*: simple, tubular.

♂. Unknown.

Distribution: ABYSSINIA.

Phlebotomus (Sergentomyia) collarti Adler, Theodor & Parrot.

P. collarti Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18: 72.

The description below is after the original description of 14 females and 7 males from Stanleyville; types and co-types are in the Hebrew University, Jerusalem, and the Institut Pasteur d'Algérie.

♀. Length: 1.4–1.8 mm. *Antenna*: formula 2/III–XV, segment III (0.15–0.20 mm.) > IV + V, AIII/E = 1.2. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.7, 5, 9.4.

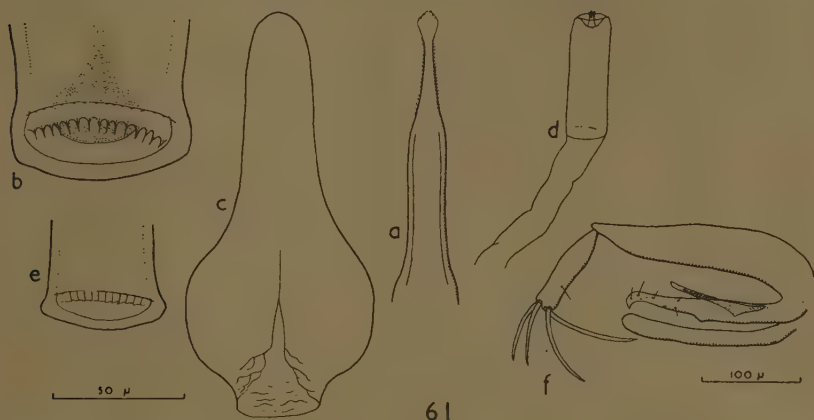


FIG. 61.—*P. collarti*, ♀: a, epipharynx; b, buccal cavity; c, pharynx; d, spermatheca. ♂: e, buccal cavity; f, terminalia. (After Adler, Theodor and Parrot, 1929.)

Epipharynx: 0.12–0.14 mm., tip expanded, not regularly tapering as in other species. *Buccal cavity*: with 10–12 equal rather large pointed teeth on an arc slightly concave posteriorly; anterior to these a row of small denticles each of which is placed opposite a space between the posterior teeth; pigmented area pale brown, subtriangular, with an anterior prolongation, sometimes absent. *Pharynx*: with a characteristic shape, three times as wide posteriorly as anteriorly, sharply constricted posteriorly, denticles inconspicuous and in optical section having the appearance of oblique scales and fine parallel folds. *Wing*: length 1.3–1.6 mm., breadth 0.3–0.38 mm., alar index 0.6–1, delta + 0.04 to + 0.12 mm. *Spermatheca*: an elongated cylindrical capsule with a very wide duct.

♂. Length: 1.4–1.5 mm., hind leg 2–2.5 mm. *Antenna*: formula 1/III–XV, segment III (0.18–0.2 mm.) > IV + V, AIII/E = 1.5–1.6. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.7, 4, 5.2, 10. *Epipharynx*: length 0.13 mm. *Buccal cavity*: with 10–12 equal teeth on an arc concave posteriorly, smaller and blunter than in the female; some small short anterior denticles. *Pharynx*: in general shape like that of *P. schwetzi*, denticles less

pointed than in the female. *Wing*: length 1.26 mm., width 0.27 mm., alar index 0.57-0.91, delta 0.04-0.1 mm. *Terminalia*: coxite (0.17-0.2 mm.) 2.5-3 times as long as style (0.75 mm.), which bears four terminal spines and small ventral seta at 0.6; paramere hooked, penis sheath cone-shaped with a blunt tip.

Distribution: BELGIAN CONGO, FRENCH CONGO, A.-E. SUDAN.

Phlebotomus (Sergentomyia) decipiens Theodor.

P. simillimus Adler, Theodor & Parrot, 1929, *Rev. Zool. Bot. afr.* 18: 72.

P. decipiens Theodor, 1931, *Bull. ent. Res.* 22: 469.

Adler, Theodor and Parrot described as *P. simillimus* Newstead a species from the Belgian Congo which agreed in its external characters with Newstead's description of that species. Re-examination of Newstead's specimens showed later that the two species were distinct and the one from the Congo was re-

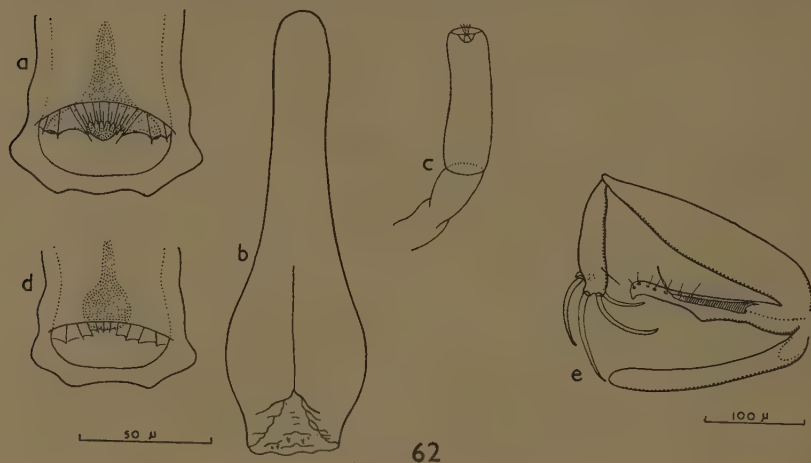


FIG. 62.—*P. decipiens*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (After Adler, Theodor and Parrot, 1929.)

described as *P. decipiens*. The account below is after the original description of 21 females and 28 males from the Congo.

♀. *Length*: 1.0-2.1 mm., hind leg 2.7-3.2 mm. *Antenna*: formula 2/III-XV, segment III > IV + V, AIII/E = 1.4-1.6. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.4, 3.6, 4.9, 8.6. *Epipharynx*: length 0.13-0.15 mm. *Buccal cavity*: with 12-14 pointed dimorphic teeth, the 4-5 median ones pointed and much straighter than the lateral ones, which are very broad and have long points, the appearance of the lateral teeth varying much according to the position in which they are mounted; pigmented plate dark brown and subtriangular with a median projection on the posterior concave margin. *Pharynx*: like that of *P. schwetzi*, but longer and narrower. *Wing*: length 1.6-1.8 mm., width 0.4-0.5 mm., alar index 1.4-2.0, delta + 0.26 to + 0.32 mm. *Spermatheca*: a cylindrical capsule with a wide duct.

♂. *Length*: 1.7-2.2 mm., hind leg 2.6-3 mm. *Antenna*: formula 1/III-XV, segment III very long > IV + V, AIII/E = 2.1-2.2. *Palp*: formula 1,2,3,4,5, relative lengths

1, 2.2, 3.7, 5, 8.6. *Epipharynx*: length 0.13–0.16 mm. *Buccal cavity*: teeth as in the female but smaller and with shorter points, pigmented plate brown, irregular and less wide at the base than in the female, sometimes absent. *Pharynx*: posterior width nearly three times anterior width and bearing fine folds. *Terminalia*: coxite (0.23–0.28 mm.) more than twice as long as style (0.1–0.13 mm.), which bears two apical and two subapical spines and small ventral seta near subapical spines; paramere hooked, penis sheath conical with blunt point.

Distribution: BELGIAN CONGO, UGANDA.

Phlebotomus (Sergentomyia) durenii Parrot.

P. durenii Parrot, 1934, *Rev. Zool. Bot. afr.* 24: 266.

P. durenii Parrot, 1939, *ibid.* 32: 145.

The description given below is after Parrot's original description of two females from Opeinge and three females from Matadi, Belgian Congo. Type specimens are in the Museum of the Belgian Congo at Tervueren.

♀. *Length*: 2.18 mm., hind leg 2.5–2.8 mm. *Antenna*: formula 2/III–XV, segment III (0.217–0.23 mm.) > IV + V, AIII/E = 1.36, ascoids short, those on IV = 0.25 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 4.2, 4.8, 10. *Epipharynx*:

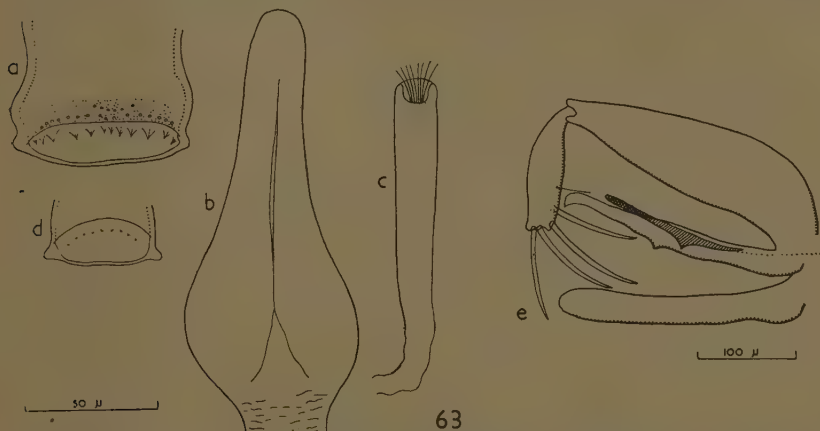


FIG. 63.—*P. durenii*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia.

length 0.16–0.17 mm. *Buccal cavity*: with 12 pointed teeth on an arc very slightly concave posteriorly, the two median teeth shorter and narrower than the others; two anterior rows of fine denticles, the first with 7 and the second with 16; pigmented plate pale brown, with no anterior prolongation. *Pharynx*: with posterior width about three times anterior width, very constricted posteriorly and with fine ridges as in *P. schwetzi*, but fewer. *Wing*: length 1.6–1.7 mm., width 0.38–0.40 mm., alar index 0.61–0.65, delta + 0.11 to + 0.13 mm. *Spermatheca*: tubular, slightly wider distally than proximally and continuing without clear demarcation into a duct of equal diameter.

♂. *Length*: 1.62–1.69 mm., hind leg 2.35–2.4 mm. *Antenna*: formula 1/III–XV, segment III (0.24–0.25 mm.) < IV + V, AIII/E = 1.66, ascoids very short, as in the female, that on IV = 0.17 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.5,

5.5, 5.9, 7. *Epipharynx*: length 0.14–0.15 mm. *Buccal cavity*: with 8–10 short pointed monomorphic teeth on an arc concave posteriorly; no pigmented area. *Pharynx*: posterior width 1.5 times anterior width, without visible folds or denticles. *Wing*: length 1.48–1.63 mm. width 0.28–0.30 mm., alar index 0.58–0.75, delta + 0.04 to + 0.1 mm. *Terminalia*: coxite (0.21–0.22 mm.) slightly more than twice length of style, which bears two terminal and two subterminal spines and anterior small seta at 0.7; paramere (0.17 mm.) as long as lateral lobe, hooked; penis sheath elongated, bluntly pointed, slightly turned up at the tip; lateral lobe 0.168–0.175 mm., unarmed.

Distribution: BELGIAN CONGO, IVORY COAST, FRENCH CONGO, A.-E. SUDAN.

Phlebotomus (Sergentomyia) squamipleuris Newstead.

P. squamipleuris Newstead, 1912, *Bull. ent. Res.* 3: 366.

P. minutus var. *africanus* Newstead, 1912, *ibid.* 3: 363.

P. squamipleuris Sinton, 1923, *Indian J. med. Res.* 11: 65; 1927, *ibid.* 15: 24.

P. ghesquieri Parrot, 1929, *Rev. Zool. Bot. afr.* 18: 90.

P. iraqi Adler & Theodor, 1929, *Ann. trop. Med. Parasit.* 23: 269.

P. squamipleuris Theodor, 1931, *Bull. ent. Res.* 22: 470.

Newstead described this species from a single female from Khartoum. In 1923 Sinton recorded this species from India and described both sexes, adding the description of the characteristic buccal armature and spermatheca in 1927. Theodor in 1933 pointed out certain differences between the African and Indian forms of the species and separated the latter from the type as *P. squamipleuris* var. *indicus*. The synonymy of *P. squamipleuris* and *P. africanus* is discussed on p. 408.

The description given here has been compiled from published descriptions of 16 female and 9 male African specimens supplemented by our own material from Khartoum and examination of one of Newstead's specimens, labelled co-type ♀, from Khartoum, which is in the British Museum.

♀. *Length*: 1.4–1.9 mm., hind leg 2.3–2.6 mm. *Antenna*: formula 1/IV–XV, segment III (0.15–0.17 mm.) < IV + V, AIII/E = 1–1.1, ascoid on IV = 0.5 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 3.8, 4.6, 8.4; Newstead's spines on segments 2 and 3. *Epipharynx*: length 0.15–0.17. *Buccal cavity*: with 36–40 long teeth, blunt in appearance but shown by dissection to be very pointed, arranged on an arc strongly convex posteriorly; pigmented plate dark brown, convex posteriorly, resembling in shape a section of an orange with a small narrow pointed paler anterior prolongation; anteriorly to the pigmented plate a pair of lateral buccal protuberances project inwardly from the wall of the buccal cavity; in specimens cleared with caustic potash a row of small anterior denticles can sometimes be seen in front of the buccal teeth (*P. iraqi*). *Pharynx*: with posterior width about four times anterior width, sharply constricted posteriorly, pigmented in the centre and bearing numerous strong denticles. *Wing*: length 1.5–1.9 mm., width 0.36–0.45 mm., alar index 1–1.3, delta + 0.12 to + 0.21 mm. Thoracic pleurae in fresh specimens are seen to bear tufts of broad scales like those seen in mosquitoes. *Spermathecae*: non-crenulated, globular, turnip-shaped covered with regular transverse rows of small spiniform projections. *Abdomen*: may show a few erect hairs on the dorsal aspects of segments II–VI, but usually all hairs are recumbent in this position.

♂. *Length*: 1.4–1.7 mm. *Antenna*: formula 1/IV–XV, segment III (0.14–0.16 mm.) < IV + V, AIII/E = 1.1, ascoid on IV = 0.28 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.5, 4.1, 4.7, 7; Newstead's spines on segments 2 and 3. *Epipharynx*: length 0.128–0.145 mm. *Buccal cavity*: with about 18 small blunt teeth slightly separated from each other; pigmented plate brown, irregularly oval, sometimes absent; lateral buccal protuberances less marked than in the female. *Pharynx*: as in the female, but

non-pigmented and with less well-marked denticles. *Wing*: length 1.5 mm., width 0.32–0.36 mm., alar index 0.93–1.28, delta + 0.10 to + 0.18 mm. Broad scales on thoracic pleurae. *Abdomen*: sixth segment large and slightly tapering. *Terminalia*: coxite (0.18–0.23 mm.) a little more than twice as long as style (0.08–0.10 mm.), which bears four terminal spines and small ventral seta at 0.6; penis sheath pointed, penis filaments bifid with bulbous expanded extremity.



FIG. 64.—*P. squamipleuris*, ♀: a, fourth antennal segment; b, buccal cavity; c, pharynx; d, pleural scales; e, spermatheca. ♂: f, buccal cavity; g, terminalia. (a and g from Sudan specimen; b and c after Theodor, 1938; d after Newstead, 1912; e and f after Parrot, 1930.)

P. squamipleuris presents a number of highly characteristic features such as the unusual antennal formula (especially in the female) the presence of scanty erect hairs on the abdominal tergites, the broad scales on the thoracic pleurae and the presence of Newstead's spines on the 2nd and 3rd palpal segments.

Distribution: ABYSSINIA, MADAGASCAR, MOZAMBIQUE, NIGERIA, A.-E. SUDAN, SENEGAL, FRENCH SUDAN, IVORY COAST, DAHOMEY, FRENCH CONGO. Also in Palaearctic Region.

Phlebotomus (Sergentomyia) squamipleuris var. *dreyfussi* Parrot.

P. squamipleuris var. *dreyfussi* Parrot, 1933, *Arch. Inst. Pasteur Algér.* 11: 603.

P. squamipleuris var. *dreyfussi* Ristorcelli, 1941, *Arch. Inst. Pasteur Maroc.* 2: 521.

P. squamipleuris var. *dreyfussi* Parrot & Durand-Delacre, 1947, *Arch. Inst. Pasteur Algér.* 25: 77.

Type locality Laghuat, Algeria; type specimen in the Institut Pasteur d'Algérie. The description below is mainly after Parrot and Durand Delacre, from ten females and one male.

♀. *Length*: 1.8–2.2 mm. *Antenna*: formula 1/IV–XV, segment III (0.17–0.21 mm.) > IV + V, AIII/E = 1.07–1.2. *Palp*: formula 1,2,3,4,5, relative lengths 1, 3.1, 4.2, 5.1, 8.4. *Epipharynx*: length 0.18 mm. *Buccal cavity*: with 42–45 monomorphic teeth on an arc convex posteriorly; pigmented plate dark brown, shaped like an irregular section of an orange with a pale triangular forward prolongation. *Pharynx*: three times as wide posteriorly as anteriorly, bearing numerous strong spines. *Wing*: length 1.7–2 mm. breadth 0.4–0.53 mm., alar index 0.68–1.1, delta + 0.085 to + 0.17 mm. *Legs*: each trochanter with short spines as described by Newstead and Sinton in *P. squamipleuris*; proximal half of each femur with short, slightly curved spines on the inner surface, 8–9 on the first femora, 5–4 on the second, and 4–3 on the third. *Spermatheca*: a turnip-shaped capsule slightly elongated with nearly parallel sides, pigmented from its junction with the duct for two-thirds of its length and very finely pubescent, larger than in *P. squamipleuris* (0.040–0.045 mm. long and 0.035–0.038 mm. wide).

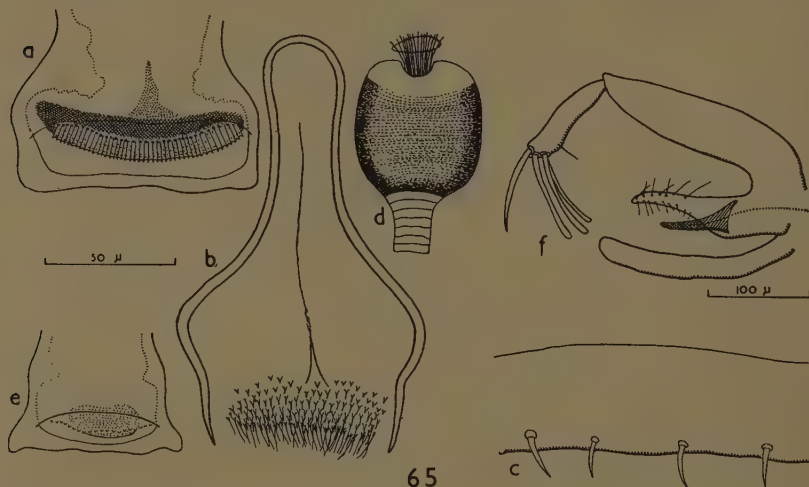


FIG. 65.—*P. squamipleuris* var. *dreifussi*, ♀: a, buccal cavity; b, pharynx; c, spines on first femur; d, spermatheca. ♂: e, buccal cavity; f, terminalia. (After Parrot and Durand-Delacré, 1947.)

♂. *Length*: 1.94 mm. *Antenna*: formula 1/IV–XV, segment III (0.23 mm.) < IV + V, AIII/E = 1.5, ascoid on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.9, 4.1, 4.5, 8.3. *Epipharynx*: length 0.15 mm. *Buccal cavity*: with 22 teeth, pigmented area and prominent lateral buccal protuberances as in *P. squamipleuris*. *Pharynx*: about twice as wide posteriorly as anteriorly armed with fine, short spines. *Wing*: length 1.84 mm., breadth 0.39 mm., alar index 0.95, delta + 0.15 mm. *Legs*: spines on all femora as in the female. *Terminalia*: coxite (0.21 mm.) more than twice as long as style (0.1 mm.), which bears two terminal and two subterminal spines and small ventral seta at 0.8; paramere 0.1 mm., penis sheath (0.08 mm.) elongated, conical with sharp point, lateral lobe 0.20 mm.

This variety differs from typical *P. squamipleuris* and its other varieties by the presence of the femoral spines in both sexes, in the male by the greater body length and greater length of AIII and higher value of AIII/E, and in the

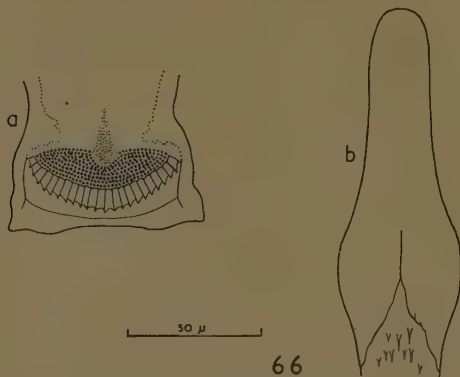
female by the number of buccal teeth, the shape of the pharyngeal armature and the large spermatheca.

Distribution: ABYSSINIA, ERITREA, also in North Africa.

Phlebotomus (Sergentomyia) squamipleuris var. *inermis* Theodor.

P. squamipleuris var. *inermis* Theodor, 1938, *Bull. ent. Res.* 29 : 165.

The description given below is after the original description from 28 females from Gadau. This variety differs from *P. squamipleuris* chiefly in the armature of the buccal cavity and pharynx.



66

FIG. 66.—*P. squamipleuris* var. *inermis*, ♀: a, buccal cavity; b, pharynx. (After Theodor, 1938.)

♀. All measurements and indices as in *P. squamipleuris*. *Buccal cavity*: with 20–24 teeth, pigmented plate like the segment of a circle with the straight side anteriorly. *Pharynx*: with posterior part less widened than in *P. squamipleuris* and hardly any armature except a few small teeth. *Legs*: no spines on the femora. *Spermatheca*: as in the type form.

♂. Unknown.

Distribution: NIGERIA, ABYSSINIA, A.-E. SUDAN.

Phlebotomus (Sergentomyia) wurtzi Parrot.

P. wurtzi Parrot, 1938, *Arch. Inst. Pasteur Algér.* 16 : 213.

The description below is after Parrot, from one female and one male from Dire Dawa, Abyssinia. Type specimens in the Institut Pasteur d'Algérie.

♀. *Length*: 2.25 mm., hind leg 3.1 mm. *Antenna*: formula 2/III–XV, segment III (0.168 mm.) = IV + V, AIII/E = 1.0, ascoids long, but not reaching beyond the tips of their segments, those on IV = 0.6 length of segment. *Palp*: formula 1,2,4,3,5, relative lengths 1, 1.8, 4.6, 3.8, 7. *Epipharynx*: length 0.168 mm. *Buccal cavity*: with three short, pointed, widely separated median teeth and on each side a dozen fine, irregular, scarcely visible denticles; pigmented plate absent. *Pharynx*: with posterior width a little less than twice anterior width and with several transverse folds. *Wing*: length 1.82 mm., width 0.44 mm., alar index 0.63, delta + 0.066 mm. *Spermatheca*: sac-like with numerous fine parallel transverse folds.

♂. Length: 2 mm., hind leg 2.62 mm. Antenna: formula 1/III-XV, segment III (0.175 mm.) = IV + V, AIII/E = 1.1, ascoid on IV about a third of its length. Palp: formula 1,2,4,3,5, relative lengths 1, 2.2, 4.7, 3.3, 7.3. Epipharynx: length 0.157 mm. Buccal cavity: without visible teeth and without pigmented plate. Pharynx: 1.5 times as wide posteriorly as anteriorly, without denticles or visible folds. Wing: length 1.56

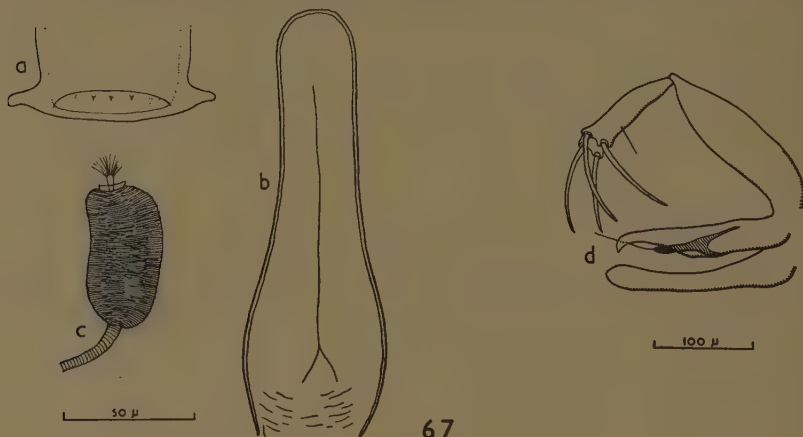


FIG. 67.—*P. wurtzi*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, terminalia. (After Parrot, 1938.)

mm., width 0.34 mm., alar index 0.7, delta + 0.09 mm. Terminalia: coxite (0.20 mm.) about twice length of style (0.098 mm.) which bears four long terminal spines and small ventral seta at about 0.7; paramere 0.164 mm., hooked; penis sheath (0.06 mm.) a little turned up towards its apex with rounded tip; lateral lobe 0.178 mm., a little shorter than coxite.

Distribution: ABYSSINIA.

Phlebotomus (Sergentomyia) horgani Lewis and Kirk.

P. horgani Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond. (B)* 15: 55.

Type specimens in the British Museum. Descriptions are based on one female and 4 males from Lake Jur and R. Zeraf, A.-E. Sudan. Theodor (1948) considered that *P. horgani* might be a synonym of *P. wurtzi*.

♀. Length: 2.6 mm., hind leg 3.6 mm. Antenna: formula 2/III-XV, segment III (0.20 mm.) = IV + V, AIII/E = 0.8, ascoids on IV = 0.5 length of segment. Palp: formula 1,2,(4,3),5, relative lengths 1, 1.6, 2.4, 2.3, 5. Buccal cavity: about five delicate pointed teeth (some may be missing), pigmented plate narrow and with irregular hind margin. Pharynx: with posterior width 1.5 times anterior width, thin walled and pigmented with a few minute ridges and spicules. Epipharynx: length 0.26 mm. Wing: length 1.8 mm., width 0.5 mm., alar index 0.8, delta + 0.14 mm. Spermatheca: a rather delicate thin-walled sac.

♂. Length: 1.8–2.1 mm., hind leg 2.5–2.7 mm. Antenna: formula 1/IV-XV, segment III (0.14–0.17 mm.) < IV + V, AIII/E = 0.9. Palp: formula 1,2,3,4,5, relative lengths

1, 2.0, 3.4, 4.2, 8.4. *Epipharynx*: length 0.19 mm. *Buccal cavity*: teeth vestigial, pigmented plate small and pear-shaped, pointed posteriorly. *Pharynx*: with posterior width twice anterior width, very lightly pigmented and unarmed. *Wing*: length 1.3–1.6 mm., width 0.28–0.30 mm., alar index 0.7, delta + 0.05 to 0.09 mm. *Terminalia*: coxite

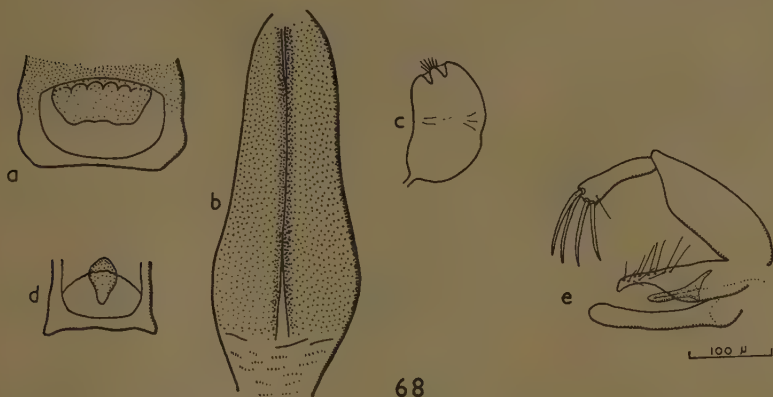


FIG. 68.—*P. horgani*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, alar terminalia. (After Lewis and Kirk, 1946.)

(0.18–0.20 mm.) about twice as long as style (0.09–0.10 mm.), which bears four terminal spines and small ventral seta at 0.9; paramere 0.10–0.14 mm., hooked; penis sheath 0.08–0.09 mm., conical and blunt, but appearing dagger-like and pointed unless its position is changed by pressure; lateral lobe 0.17–0.18 mm.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) lewisi Parrot.

P. lewisi Parrot, 1948, *Arch. Inst. Pasteur. Algér.* 26: 121.

The description given is after Parrot's original description. The species is known from one female only, from Abri, A.-E. Sudan. The type specimen is in the British Museum (Natural History).

♀ (damaged). *Antenna*: formula 2/III–XV, segment III (0.20 mm.) > IV + V, AIII/E = 1.23, ascoids very short and with rounded tips, those on IV = 0.2 length of segment. *Palp*: formula 1,2,(3,4),5, relative lengths 1, 3.3, 4.8, 4.8, 8; modified spines of Newstead only on proximal third of segment 3. *Epipharynx*: length 0.162 mm. *Buccal cavity*: with 21 pointed equal monomorphic teeth in a straight line; anteriorly a row of 21 strong round denticles, each placed about opposite an interdentary space; more anteriorly, and laterally, two groups of 6–7 smaller denticles; pigmented plate dark brown, shaped like an irregular ellipse, elongated transversely and reaching the sides of the buccal cavity, with an anterior, paler, broad, truncated extension; two well-developed pre-buccal lateral processes, pointing inwards and with irregular inner margins. *Pharynx*: posterior width about 2.5 times anterior width, sharply constricted at the posterior end, which bears numerous strong spines with long points. *Wing*: length 1.77 mm., width 0.51 mm., alar index 0.81, delta + 0.136 mm. *Spermatheca* as in *P. squamipleuris*, a poppy-head shaped body, apparently smooth.

♂. Unknown.

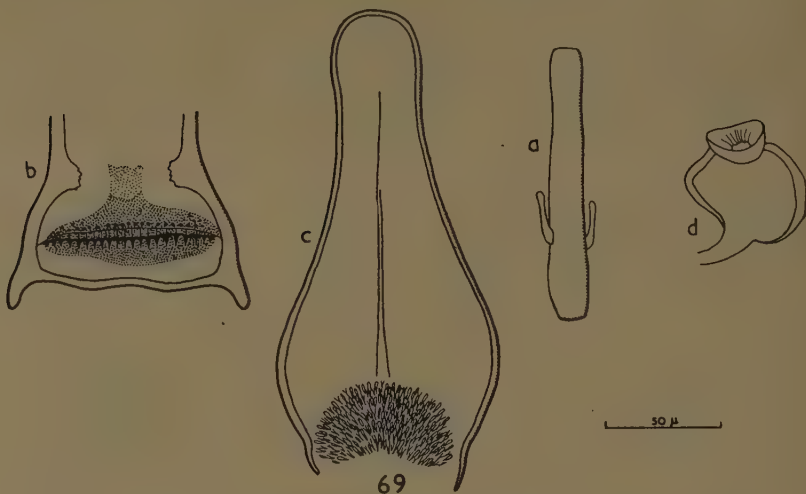


FIG. 69.—*P. lewisi*, ♀: *a*, fourth antennal segment; *b*, buccal cavity; *c*, pharynx; *d*, spermatheca. (After Parrot, 1948.)

Variation. A female from Agordat, in Eritrea, possibly of this species, has been examined by Dr. L. Parrot. He noted that the antennal ascoids were a little less spatuliform and the buccal denticles less conspicuous than in the type.

Distribution: A.-E. SUDAN, ERITREA.

Phlebotomus (Sergentomyia) hunti Lewis and Kirk.

P. hunti Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond. (B)* 15: 55.

From the original description of 6 females and 3 males from Li Yubu, A.-E. Sudan. Type specimens in the British Museum.

♀. *Length*: 2.7–3.4 mm., hind leg 4.7–4.9 mm. *Antenna*: formula 2/III–IX (distal segments missing), segment III (0.41–0.42 mm.) > IV + V, AIII/E = 1.6, ascoids on IV = 0.3 length of segment. *Palp*: formula 1,2,3,4, (5 missing), relative lengths 1, 2.5, 3.8, 5.2. *Epipharynx*: length 0.26–0.28 mm. *Buccal cavity*: with no normal teeth but with numerous tooth-like thickenings in the position occupied by the anterior denticles of many species; pigmented plate very wide, extending to the sides of the cavity, with a short forward pale projection, hind margin variable in shape, smooth or irregular. *Pharynx*: with posterior width twice anterior width, slightly constricted, at hind end armed with minute spicules. *Wing*: length 2.21–2.36 mm., width 0.64–0.73 mm., alar index 2.2, delta + 0.44 to + 0.55 mm. *Spermatheca*: thin-walled and sub-cylindrical, broader distally.

♂. *Length*: 2.7–3.2 mm. *Antenna*: formula 1/III–V (distal segments missing), segment III (0.49 mm.) > IV + V, AIII/E = 2.0, ascoid on IV = 0.2 length of segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 2.8, 4.5, 5.7, —. *Buccal cavity*: with three rows of punctiform denticles about 8, 15 and 18 in number; about six minute pointed teeth; pigmented plate small, oval and ill-defined. *Pharynx*: as in female. *Epipharynx*: length 0.24 mm. *Wing*: length 2.13–2.16 mm., breadth 0.55–0.59 mm., alar index 2.1, delta + 0.41 to 0.43 mm. Genital pump in segment VI. *Terminalia*: coxite (0.34–0.38

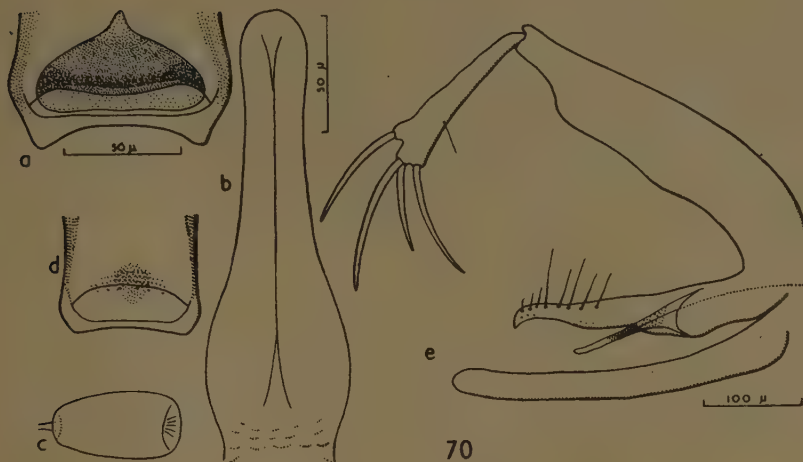


FIG. 70.—*P. huntii*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. ♂: *d*, buccal cavity; *e*, terminalia. (*a* from Sudan specimen; *b*–*e* after Lewis and Kirk, 1946.)

mm.) 2·2 times length of style (0·16–0·17 mm.), which bears four terminal spines and small ventral seta 0·7; paramere 0·21–0·24 mm.; penis sheath 0·14–0·15 mm., conical, bluntly pointed and turned up at the tip, with pigmented centre and clear tip; lateral lobe hooked.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) rutledgei Lewis and Kirk.

P. rutledgei Lewis & Kirk, 1946, *Proc. R. ent. Soc. Lond. (B)* 15: 55.

This species is known from one female only, from the Zeraf River, A.-E. Sudan. Type specimen is in the British Museum.

♀. Length: 1·8 mm., hind leg 2·2 mm. Antenna: formula 2/III–XII (other segments missing), segment III (0·08 mm.) < IV + V, AIII/E = 0·5, ascoids on IV more than half

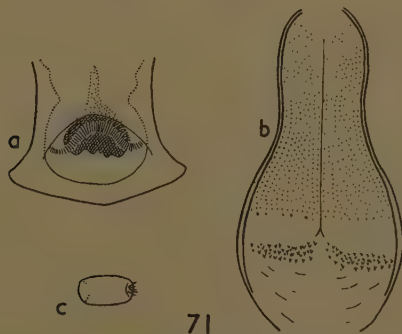


FIG. 71.—*P. rutledgei*, ♀: *a*, buccal cavity; *b*, pharynx; *c*, spermatheca. (After Lewis and Kirk, 1946.)

length of the short thick segment. *Palp*: formula 1,2,3,4,5, relative lengths 1, 1.9, 3.1, 4.2, 8.8. *Epipharynx*: length 0.17 mm. *Buccal cavity*: with about 50 very fine teeth on an arc deeply concave posteriorly, most of them pointing radially inwards and the outer ones pointing backwards; some ill-defined denticles at the bases of some of the teeth; pigmented plate much narrower than buccal cavity, with long narrow forward extension and very uneven posterior margin. *Pharynx*: with posterior width twice anterior width, somewhat constricted before the middle, slightly pigmented in anterior two-thirds; dorsal plate with faint ridges, ventral plates with a transverse band of delicate but conspicuous pointed teeth. *Wing*: length 1.37 mm., width 0.28 mm., alar index 0.6, delta + 0.03 mm. *Spermatheca*: simple, tubular.

♂. Unknown.

Distribution: A.-E. SUDAN.

Phlebotomus (Sergentomyia) lumsdeni Kirk & Lewis.

P. lumsdeni Kirk & Lewis, 1950, *Proc. R. ent. Soc. Lond. (B)* 19: 11-13.

♀. *Length*: 1.9 mm. *Antenna*: missing. *Palp*: formula 1,2,4,3,5, relative lengths 1, 2.4, 5, 4, 12.4. *Epipharynx*: length 0.2 mm. *Buccal cavity*: with 15-16 teeth on an arc strongly concave posteriorly; the median one or two teeth are small, short and straight, differing from the lateral ones which are very large pointed and curved, so that their points are directed medially and posteriorly, those nearest the median teeth being directed more

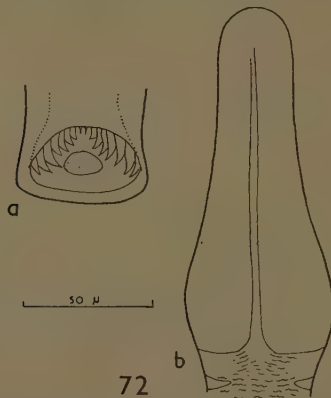


FIG. 72.—*P. lumsdeni*, ♀: a, buccal cavity; b, pharynx. (After Kirk and Lewis, 1950.)

medially than the extreme lateral ones, which are directed more posteriorly; pigmented area faint and indistinct. *Pharynx*: about twice as wide posteriorly as anteriorly, lamp-glass shaped, with an armature of transverse wavy ridges and, laterally, occasional squamous spines with the points directed medially. *Wing*: length 1.6 mm., width 0.55 mm., alar index 1.8, delta + 0.07 mm. *Spermatheca*: simple, tubular, poorly chitinized, without annulations.

♂. Unknown.

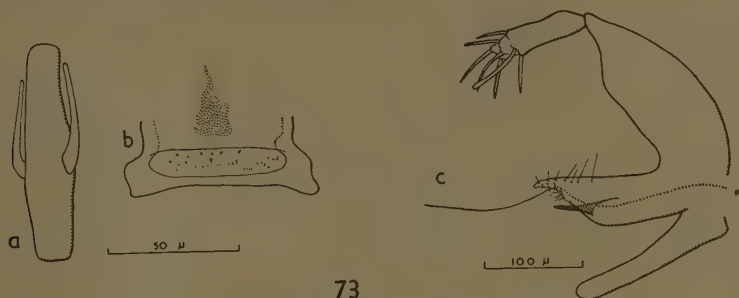
The female of *P. lumsdeni* is distinguished from all the other Ethiopian species by the characteristic morphology of the buccal teeth. Type specimen (one ♀ only) is in the British Museum.

Distribution: UGANDA.

Phlebotomus (Sergentomyia) hirtus Parrot & de Jolinière.

P. hirtus Parrot & de Jolinière, 1945, *Arch. Inst. Pasteur Algér.* 23 : 56.

Type specimen, from the Ahaggar, in the Institut Pasteur d'Algérie. This species is known from one male only which is readily distinguishable from all the other Ethiopian species by the presence of seven spines on the style. Theodor (1948) considered it might be an abnormality. The description given below is after Parrot and de Jolinière.



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FIG. 73.—*P. hirtus*, ♂ : a, fourth antennal segment ; b, buccal cavity ; c, terminalia. (After Parrot and De Jolinière, 1945.)

♀. Unknown.

♂. *Length* : 2.62 mm., hind leg 2.8 mm. *Antenna* : formula 2/III-XV, segment III (0.14 mm.) = IV + V, AIII/E = 0.67, ascoids on IV = 0.5 length of segment. *Palp* : formula 1,2,4,3,5, relative lengths 1, 2.5, 4.5, 3.2, 5. *Epipharynx* : length 0.21 mm. *Buccal cavity* : with two median rows and two lateral groups of short, pointed and irregularly arranged teeth ; pigmented plate triangular with base posteriorly. *Pharynx* : posterior width twice anterior width, unarmed. *Wing* : length 1.82 mm., width 0.36 mm., alar index 0.61, delta + 0.017 mm. *Terminalia* : coxite (0.2 mm.) twice as long as style, which bears seven spines, some of which are spatulate ; paramere (0.153 mm.) shaped like the prow of a ship ; penis sheath short (0.08 mm.) ; lateral lobe 0.168 mm.

Distribution : AL AHAGGAR.

Phlebotomus (Sergentomyia) mirabilis Parrot & Wanson.

P. mirabilis Parrot & Wanson, 1939, *Rev. Zool. Bot. afr.* 32 : 149.

P. mirabilis Parrot & Wanson, 1946, *Arch. Inst. Pasteur Algér.* 24 : 143.

The type specimens, from Thysville, are in the Museum of the Belgian Congo at Tervueren. The description below is after Parrot and Wanson (1946) from 7 females and 6 males.

♀. *Length* : 2.2–3.2 mm., hind leg 4.4–5.2 mm. *Antenna* : formula 2/III-XV, segment III (0.35–0.38 mm.) < IV + V, AII/E = 1.2–1.3, ascoids long extending beyond the tip of the segments. *Palp* : formula 1,4,2,3,5, relative lengths 1, 3.4, 4.4, 2.7, 7. *Epipharynx* : length 0.27–0.29 mm. *Buccal cavity* : with 10–14 pointed teeth spread out like a fan, the median teeth being bigger than the laterals ; no pigmented plate. *Pharynx* : about twice as wide posteriorly as anteriorly, armed with fine transverse folds. *Wing* : length 2.55–2.67 mm., width 0.76–0.85 mm., alar index 1.1–1.4, delta + 0.17 to 0.20 mm. *Spermatheca* : in the form of a sac bent over like a phrygian cap with thin walls dilated at its

opening into the duct, which is heavily chitinized and pigmented and opens separately into the vulva.

♂. Length: 2.23-3 mm., hind leg 4.84-4.92 mm. Antenna: formula 2/III-XV, segment III (0.41-0.45 mm.) < IV + V, AIII/E = 1.5-1.8, ascoids long, but do not extend beyond tips of segments. Palp: formula 1,4,2,3,5, relative lengths 1, 3.3, 4.4, 3, 7.3. Epipharynx: length 0.23-0.24 mm. Buccal cavity: with 8-12 strong pointed teeth; no pigmented area. Pharynx: 1.5 times as wide posteriorly as anteriorly and with some transverse ridges in its posterior part. Terminalia: coxite (0.3-0.34 mm.) 1.25 times as

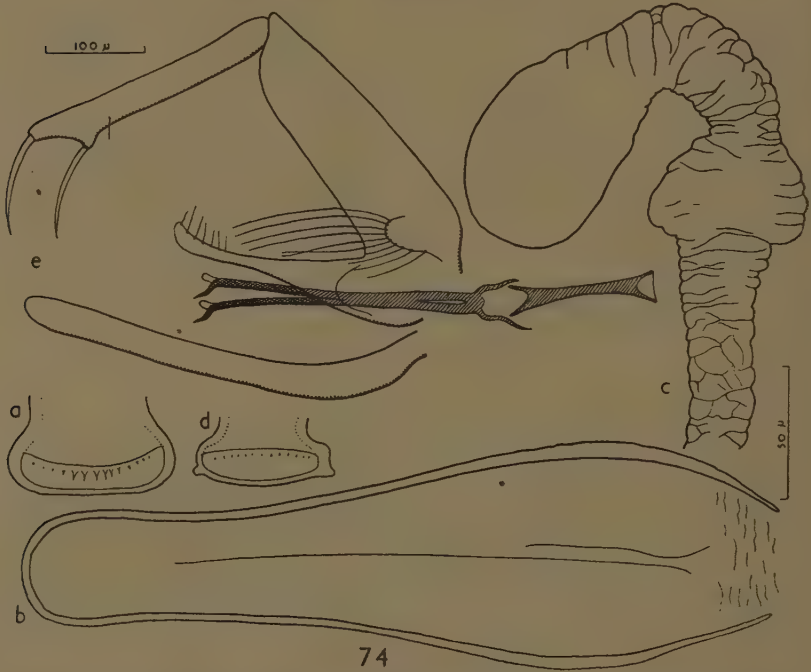


FIG. 74.—*P. mirabilis*, ♀: a, buccal cavity; b, pharynx; c, spermatheca. ♂: d, buccal cavity; e, terminalia. (a-d after Parrot and Wanson, 1946; e after Theodor, 1948.)

long as style (0.26 mm.) and bearing on its internal surface near the base a tuft of hairs, arising from a short peduncle; style bears two spines, one terminal the other, at about 0.7, with small ventral seta at 0.6; paramere (0.25 mm.) hooked, penis sheaths apparently fused together, penile filaments with dilated hyaline tip and subapical process; lateral lobe (0.39-0.40 mm.) longer than coxite.

Phlebotomus mirabilis, by its numerous unusual features is immediately differentiated from all other species.

Distribution: BELGIAN CONGO, UGANDA.

As pointed out to us by Professor O. Theodor, the Uganda specimens are not identical with the type form and require further study.

ADDENDUM.

Since this paper was submitted for publication a new Ethiopian species, *P. wynnæ*, has been described by Watson (1951). It has not been possible to include *P. wynnæ* in the diagnostic tables, but a description of the species is given below (after Watson, by permission of the *Annals of tropical Medicine and Parasitology*).

Phlebotomus (Sergentomyia) wynnæ Watson.

P. wynnæ Watson, 1951, *Ann. trop. Med. Parasit.* 45: 78.

♀. Length: 1.9 mm., hind leg 2.81 mm. Antenna: segment III = 0.17 mm., < IV + V, AIII/E = 0.83, formula 2 III-IX . . . (distal segments missing), ascoids long, those on IV = 0.6 length of segment. Palp: formula 1,2,4,3,5, relative lengths 1, 3, 5, 4.2, 11.8. Epipharynx: length 0.2 mm. Buccal cavity: heavily armed with approximately 30 teeth borne on an arc concave posteriorly, in three groups of 10, the median ones being heavier and more widely spaced than the lateral ones; the extreme lateral teeth point slightly towards the mid-line; pigmented area absent. Pharynx: lampglass shaped, wide median part 3.3 times as wide as narrow anterior and posterior parts, armed with peculiar ridges restricted entirely to narrow posterior part; pigmented mid-line. Wing: length 1.7 mm., width 0.6 mm., alar index 1.1, delta = 0.05 mm. Spermatheca: not visible, therefore presumably simple and thin-walled.

♂ Unknown.

P. wynnæ is readily distinguished from all other Ethiopian species by the morphology of the buccal cavity and pharynx. The type specimen is in the British Museum.

Distribution: UGANDA.

METHODS.

COLLECTING.

The adult flies can often be obtained with suction catchers or tubes in darkened parts of houses, stables and latrines. They may often be driven from animal burrows by tobacco smoke or a handful of dust. Many can be caught at light, but these are not fully representative of the local fauna.

Very useful traps are simply made with oiled paper. A piece of paper is placed in a cleft stick, smeared with castor oil, and the stick stuck in the ground at dusk, usually near a hole or crack in the soil. In the morning pieces of the paper with sandflies attached are either placed in formalin for storage, or are put in spirit which washes off the flies. When the insects are abundant traps in any situation will catch them.

Species which bite mammals can be caught with oiled paper or taken alive in a sandfly net with a few holes in it placed over a cage containing a monkey or guinea-pig.

Sinton (1932a) found that the best method of storage was to keep the insects dry in tubes. Those preserved in 70 per cent. alcohol became brittle and difficult to treat with caustic potash.

MOUNTING.

For permanent preparations Sinton recommends placing a specimen in a watch glass, wetting it with a single drop of 70 per cent. alcohol, and immediately adding ten per cent. caustic potash which is left overnight or for 12 hours or more. The insect is then washed in three or four changes of water, each lasting 15 to 30 minutes, stained with carbol fuchsin, and finally mounted in Canada balsam.

For rapid examination sandflies may be dissected in Langeron's chlor-lacto-phenol which clears them. Its composition (Sinton, 1933) is :

Chloral hydrate (crystals)	2 parts
Acid, carbolic (crystals)	1 part
Lactic acid, pure	1. „

The insect can later be mounted in Puri's medium, the composition of which is given by Hopkins (1936) as follows :

Water	10 c.c.
Gum acacia (picked lumps, not the powdered form)	8 grammes
Chloral hydrate	70 „
Glycerine	5 c.c.
Acetic acid (glacial)	3 „

The ingredients should be dissolved in the above order, on a water bath at about 80° C. We then filter the fluid through a wad of cotton wool at the bottom of a funnel in a tin kept warm by the heat of the sun or other means. Under Sudan conditions preparations made with this medium seldom require to be ringed with cement if enough Puri's medium is used at the time and after a few days. Canada balsam should never be used for ringing this medium.

De Meillon and Lavoipierre (1944) heated specimens in potash for an hour, left them in it cold overnight, transferred them to chlor-lacto-phenol with a little one per cent. aqueous acid fuchsin, placed them in the same fluid with filter paper to prevent later crystallization of phenol, and dissected and mounted them in de Faure's medium.

When we examine large numbers of flies and keep them for future reference, we place each one straight in a drop of Puri's medium, cut off the head and place it ventral surface upward, and cover the drop with a $\frac{3}{8}$ inch circular cover glass, applying a thick ring of Puri's medium a day or two later. Under Sudan conditions, such preparations, which only take a few seconds to make, appear to be permanent. If further dissection is required, the slide can be wetted and placed overnight in a petri dish containing a little water.

When the structure of a species is such that dissection is necessary to show some feature, we use an ordinary pointed dissecting needle and a flattened one, and a pair of similar but much smaller ones made by sharpening minute entomological pins and mounting them in handles like those of the large needles. It is usually advantageous to allow the fly's hairs to come off and so expose other structures clearly. The fly, usually unstained, is dissected in chlor-lacto-phenol or Puri's medium. To remove the buccal structures and pharynx, the insect is turned on its side, the thorax steadied with one needle and the clypeus transfixed from side to side with the other (Sinton, 1932a). By gently drawing on the clypeal needle one can remove the internal structures required.

If the pigmented area is opaque the buccal armature may have to be separated from it. When the shape of the pharynx is important it may be mounted separately beneath a supported cover glass.

The body of a female is usually mounted without further manipulation apart from flattening one or both wings. The spermatheca can usually be seen through the body wall, but must sometimes be dissected out.

The terminalia of males are usually left on the abdomen, but it is often advisable to remove the coxite and style of one side.

Dissection of Sandflies to Search for Parasites.

Sinton (1932a) recommends that the fly should be shaken up in a small quantity of saline solution to kill and wet it and remove many of the hairs. The fly is then placed in a drop of normal saline on a slide. The head is carefully separated from the thorax by placing one needle across the base of the head and the other across the front of the thorax and pulling the head forward. The anterior part of the gut is thus drawn out, still attached to the head and the unbroken mid-gut. The abdomen is nicked on either side near the tip, and the hind gut is drawn out and cut through near the anus. The gut is then drawn forward through the thorax by pulling the head forward.

Estimation of Age.

The degree of digestion of the blood and the state of the ovaries provide some information on the minimum age of the female fly. The remains of a peritrophic membrane within the mass of blood in the mid-gut shows that at least one meal has been taken previously. Adler and Theodor (1935) showed that granules appeared in the accessory glands of *P. perniciosus* shortly after feeding. The presence of these granules in a fly shows that it has emerged some time previously.

Breeding Phlebotomus in Captivity.

Colonies of *Phlebotomus* have been maintained in laboratories by several workers. Unsworth and Gordon (1946) have reviewed their methods, and described their own work on *P. papatasi*, and the following account is abstracted from their work.

Whittingham and Rook (1922) were the first to establish a colony of *P. papatasi* which they bred for three or more generations in Malta, using a chamber containing earth and stones with moist organic matter for oviposition and larval development. Smith (1925) and later Young *et al.* (1926) and Napier and Smith (1926), confined naturally-fed female flies in glass cylinders and, after two or three days, transferred them to other cylinders standing on a damp plaster of Paris tray containing pebbles and rabbit faeces as food for the larvae. After the eggs had hatched, the cylinders were replaced by an earthenware cover to ensure moisture and darkness for the larvae. Christophers *et al.* (1926), instead of plaster of Paris, used Petri dishes lined with damp filter paper bearing food for the larvae. Shortt *et al.* (1926) substituted

earthenware saucers for Petri dishes and added a little dried blood to the rabbit and goat faeces used for larval food. Ashner (1927) found that this grew moulds, and used one part of garden soil and two parts of rabbit faeces, mixed with water and stirred while drying. The flies of most laboratory colonies have been fed on human blood, but Wanson (1942) used lizards. Smith *et al.* (1940) fed the flies first on human blood and subsequently on raisins. All the work done on breeding *Phlebotomus* emphasizes the importance of maintaining a high humidity without allowing water to condense and entangle the flies.

Unsworth and Gordon (1946) bred *P. papatasi* in England in an incubator at 30° C. using two different methods the second of which was adopted to reduce labour.

In the first method newly emerged males and females were placed in lamp-glasses each containing a white card for flies to rest on. The glasses were closed at the narrow end by cotton wool plugs and at the wide end by organdie with small holes for introducing the flies. The flies were daily given an opportunity of feeding from the human arm, and between meals the wide ends of the glasses were covered with damp lint. Gravid females were transferred to lamp-glasses, of which the narrow ends were placed in small earthenware pots surrounded by damp soil, the space between the glass and the side of the pot being packed with damp cotton wool. The wider ends of the glasses were covered with damp lint. After eggs had been laid the pots were covered with damp lint and left to await hatching. Three or four days after oviposition a little food, consisting of one part of garden soil and two parts of rabbit faeces, was added. A little water was added to the earth in which the pots were embedded so that the larval food remained damp and crumbling, but not too wet. When pupae appeared the pots were uncovered and placed in cages for emergence.

The second method, devised to save time, involved the use of a single piece of apparatus, designed on the principle of a rodent burrow, and on the use of baby rats for feeding the females. A block of porous cement, measuring six inches in each dimension, was fitted with a removable roof which covered an elongated chamber, narrower at one end than the other and open at both ends. Two cylindrical wells, containing water, kept the block and chamber moist. Wooden supports carried two cages which closed the ends of the chamber. The larger cage had a sleeve, and the smaller a small hole for introducing flies. The floor of the chamber was covered with larval food. Every morning a baby rat, less than three weeks old, was placed on a piece of cork on which it was lightly restrained by mosquito netting. The cork was then placed in the chamber, supported on ridges made for the purpose.

Several observations were made on flies while they were bred by the first method. Usually, except on the day after emergence and the two days preceding oviposition, the female either fed in 20 minutes or refused for that day. Most flies took four meals before oviposition, but this number varied from one to five. Eggs were laid from seven to 12 days after emergence, the number of eggs, in 48 flies, varying from three to 66, with an average of 19, the number usually being between 20 and 30. The incubation period was about six days, and most larvae pupated after 25 to 30 days. The average length of the life-cycle from egg to adult was about six weeks, and 28 to 57 per cent. of the eggs eventually produced adults.

Keeping Adults in Captivity.

Where sandflies are abundant it may be unnecessary to breed them, but necessary to keep females alive in captivity for studies on their parasites or their physiology. As in breeding the flies a high humidity without any film of water is important. Waterston (1922), Patton and Hindle (1927), and others achieved these conditions by confining sandflies in damp earthenware pots.

Shortt *et al.* (1926) kept gravid flies alive for four or five days in lamp glasses standing on damp filter paper.

According to Smith *et al.* (1940) *P. argentipes* could be kept alive for a time in a cage with a watch-glass containing a pad of cotton wool soaked in a sterile five per cent. solution of glucose. They found, however, that bacteria soon grew in the glucose and infected the flies, so tried fruit juices and found that raisins were useful. These were washed for half an hour and scalded for a minute, and then supplied to flies kept in lamp glasses. About 50 per cent. of flies, which had taken a first meal on a kala-azar patient and then been fed on raisins, were alive after ten days, but Unsworth and Gordon (1946) achieved comparable results with *P. papatasi* without raisins.

Kirk and Lewis (1949) kept sandflies singly in tubes at a constant temperature and constant high humidity, so that no condensation occurred and the conditions could easily be repeated. Each tube measured 5 by 2.3 cm., was closed with muslin, and contained a piece of filter paper to support the fly and absorb its faeces. The tubes were placed over a solution of caustic potash giving a relative humidity of 90 per cent. in a desiccator which was kept in an incubator at 27°C. *P. orientalis* and *P. clydei* were caught after a blood meal and a considerable proportion kept in this way lived over a week without food.

It was found necessary to take careful precautions against contamination of the tubes by DDT used for mosquito control operations in the neighbourhood.

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THE ANATOMY AND MORPHOLOGY OF THE EARLY STAGES OF
CULICOIDES NUBECULOSUS MEIGEN (DIPTERA: CERA-
 TOPOGONIDAE = HELEIDAE).

By J. W. H. LAWSON, B.Sc., Ph.D.

(Department of Zoology, The University of Glasgow.)

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With 1 Plate and 46 Text-figures.

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INTRODUCTION.

CONTRIBUTIONS to the biology of the adult of *Culicoides nubeculosus* Meigen have been made by Downes (1950) and by Roberts (1950).

The larva and pupa have already been described, though not in detail, by Mayer (1934). The present work offers a more detailed description, and attempts to trace the relations of the sclerites of the larval head and of its very curious internal structures to those found in the larvae of some other families of the nematoceran Diptera.

These head skeletal structures, the so-called "hypopharynx," closely resemble those found in *Forcipomyia* and described by Frew (1923) and Saunders (1924), and appear to be peculiar to the CERATOPOGONIDAE. It has

been possible, however, to learn something of their origins from a study of the descriptions of the larvae of other families; but, of necessity, this study has fallen much short of being exhaustive. I particularly regret not having had the opportunity to examine larvae of the exotic genus *Leptoconops*, in which the head appears to be composed of only a few sclerotized struts. It is very likely that this apparently simple structure of the head of *Leptoconops* is secondary rather than primitive; but the possibility that it would yield valuable morphological information is not to be disregarded.

THE EGG.

In the laboratory females of *C. nubeculosus* laid batches of rather more than two hundred eggs. They were laid on damp filter-paper, not in any regular pattern, but scattered in a wandering line, with clusters here and there. Hatching took place on the morning of the second day after laying, so that the time of development, at room temperature, was more than 48, but less than 65 hours.

The egg itself (fig. 1) is dark brown, elongate and slightly curved, about 460 microns long by 80 microns wide. At hatching, a small cap splits off from the anterior end and the opening is further enlarged by a short longitudinal slit. The initial stages of hatching have not been observed, but several times the hatching larvae have been found half out of the chorion, from which they escaped altogether by pulling themselves along by the pro-thoracic pseudopod.

Observation of the living, developing embryo was difficult because of the deep pigmentation of the chorion. At $17\frac{1}{2}$ hours before hatching the eye-spots were visible as red-brown spots, the fore-gut was open at the mouth, showing two small diverticula within the head, which was already delimited, and the labrum and mandibles were clearly marked off (fig. 2, A). At 13 hours before hatching the ventral anterior invagination was no longer visible, while the dorsal invagination had developed a backwardly curved projection within its cavity. At 12 hours before hatching this projection had become two sclerotized hooks and the eye-spot was more complex (fig. 2, B). These hooks probably represent the epipharynx. At $8\frac{1}{2}$ hours before hatching a pair of diverticula appeared on each side of the mouth (fig. 2, C). These probably represent the hypopharynx. Shortly before this, general movements, including swallowing, became frequent, so that close and continued observation was no longer possible.

THE LARVA.

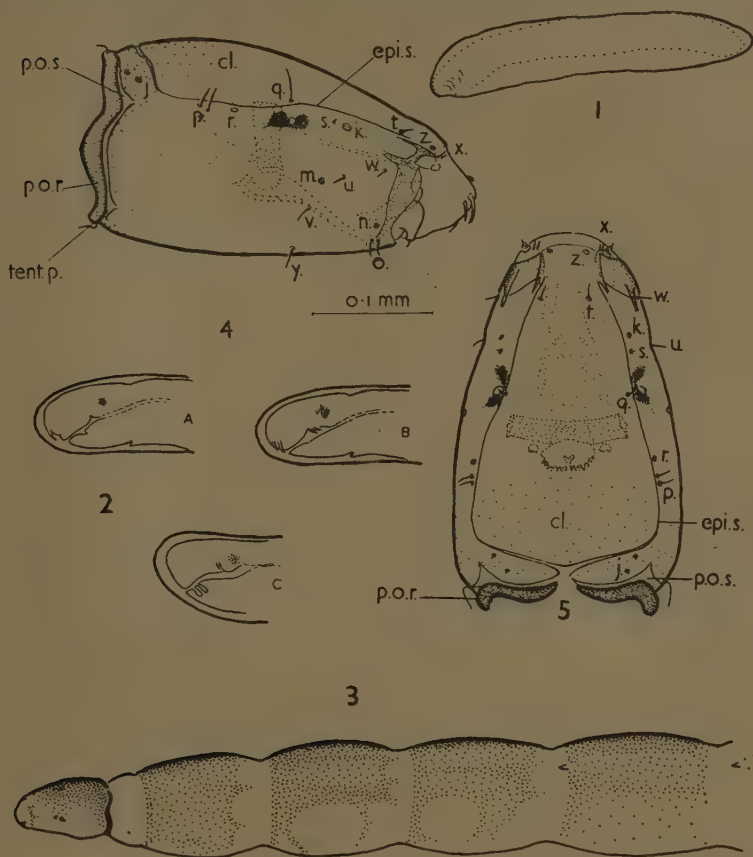
General.

Habitat: Larvae of *C. nubeculosus* have been found by Mr. Downes near a farm, swimming and burrowing in large numbers in hoofprints and other depressions filled with liquid very rich in the seepage from cow byres. This activity is unusual in *Culicoides*.

Associated with this species were *C. stigma* Meigen and possibly *C. circumscriptus* Kieffer, both in very small numbers. There were also very small numbers of larvae, especially early instars, not separated from *C. nubeculosus* except by the differences in the details of the pharyngeal skeleton, the "hypopharynx."

The 4th instar larva of *C. nubeculosus* (fig. 3) is an active and powerful

swimmer, elongate and cylindrical, up to 7.0 mm. long and 0.5 mm. wide in the biggest segment, the second abdominal, from which it tapers gradually to each end. The sclerotized, conical head is followed by a short "neck," which undoubtedly belongs to the prothorax, and then by the three thoracic and nine



FIGS. 1-5.—(1) The egg of *Culicoides nubeculosus*. (2) The anterior end of the embryo seen through the chorion: A. 17½ hours before hatching; B. 12 hours before hatching; C. 8½ hours before hatching. (3) The pigment pattern of a 4th instar larva, as seen in a preserved specimen. (4) Lateral view of the head of a 4th instar larva. *cl.*, fronto-clypeus; *epis.*, epicranial (ecdysial) suture; *p.o.r.*, post-occipital ridge; *tent.p.*, posterior tentorial pit. Other letters represent setae and sensillae. (5) Dorsal view of the head. Lettering as in fig. 4.

abdominal segments. The anal segment is clearly defined and is without ganglion and spiracles. There are neither prothoracic nor anal pseudopods. There is a pair of anal processes, of the type usually regarded as anal blood-

gills, each subdivided into four lobes. These processes are normally held extruded, but very often, when the larva is stimulated, either mechanically as by the pressure of a coverslip or, more particularly, chemically, as by the action of a fixative, they are withdrawn, either partially or completely, into the anus.

Viewed dorsally, the larva has a rather dirty light brown colour from end to end, except in the penultimate segment, where the partial absence of the pigment enables the heart to be observed. Ventrally, this pigment is absent, so that there the larva is pale and translucent. In the abdomen the disappearance of this pigment takes place gradually, while in the thorax there are clearly marked boundaries, concave downwards. These boundaries have a definite relation to the imaginal buds, bordering them on the dorsal side of their attachment to the body wall (fig. 3).

The larva is apneustic, but there are ten pairs of vestigial spiracles, one pair in the prothorax, the metathorax and each of the first eight abdominal segments. In all these segments, except the eighth abdominal, the vestigial spiracle is closely related to one of the setae.

The body setae, especially those of the abdomen, are small and in some cases minute, so that they were found only by searching with an oil-immersion objective.

The Head.

The head is well sclerotized and heavily pigmented, of a darker but clearer brown than the body. From above (fig. 5) it appears roughly triangular, with the corners well rounded, the apex at the anterior end. Average dimensions in the last (fourth) instar are : length 312 microns, breadth 207 microns. From the side (fig. 4) the ventral outline is almost straight and is parallel to the long axis of the body. Dorsally, the head first slopes upwards from behind to its highest point about one-third of its entire length from the posterior margin, and then slopes forwards and downwards to the anterior end, where it curves abruptly down into the membranous labrum. Posteriorly, at the foramen magnum, it is almost completely ringed by a narrow collar (*p. o. r.*), heavily pigmented and sclerotized, to which various muscles of the head and prothorax are attached.

In the mid-dorsal line there is a narrow gap in the collar, and from this there runs forward a suture dividing almost immediately to form two widely diverging arms which, laterally, bend sharply forwards and slightly inwards, and thereafter pursue an almost straight course, terminating anteriorly just mesad of the antennae. This is the epicranial, "frontal," or ecdysial suture (fig. 5, *epi. s.*). The only other suture is a pale narrow line immediately anterior to and following the course of the collar, except on the ventral side, where the collar is directly continuous with the ventral wall of the capsule. This is probably the post-occipital suture (figs. 4 and 5, *p. o. s.*). Above and below the mid-lateral line on each side the suture widens out into a small clear space. Muscles of the head and of the prothorax are attached in this region.

The collar itself, the post-occipital ridge (figs. 4 and 5, *p. o. r.*), does not form a simple ring round the head, but on each side, from mid-dorsal to mid-ventral has a double S curve, inclined at a slight angle to the transverse plane, so that the mid-dorsal point is slightly anterior to the mid-ventral point. The small

clear areas of the post-occipital suture occur just anterior to the forward portions of the curve. In the latero-ventral region of the collar there is a thickening extending slightly into the interior of the head. An indication of a pit is present externally, so that this is to be regarded as the posterior tentorial pit and the remains of the posterior arm of the tentorium (fig. 4, *tent. p.*).

Anteriorly, there is another ring, not so thick nor quite so heavily sclerotized as the post-occipital ridge, but broader, to which the mouth-parts articulate. This will be referred to as the sub-genal band.

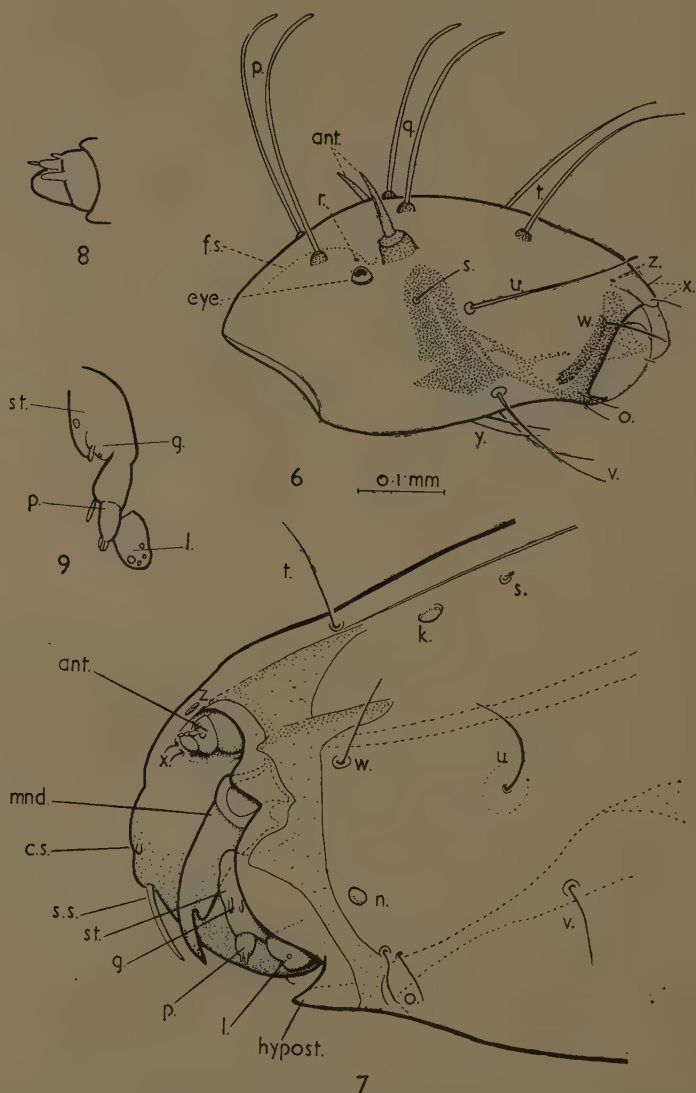
The head capsule is composed of two sclerites, separated by the ecdysial suture. The dorsal median sclerite, bounded posteriorly and laterally by the ecdysial suture, may be regarded as the fronto-clypeus, from the origin of certain muscles upon it and from its relation to the suture and to the position of the frontal ganglion. The other sclerite constitutes the rest of the capsule, forming the lateral and ventral walls. The lateral walls are to be regarded as the post-genae, while the ventral wall is formed by a forward extension of the post-occiput. The reasons for these conclusions are discussed in the section on morphology.

The eyes are situated on the upper lateral walls, just outside the ecdysial suture and about half-way along the head. Each is densely pigmented black and is hollow laterally, the concavity containing a single simple lens. There is a small, relatively clear window in the capsule in this region, but this is seen only in specimens that have been treated with potash.

1. The Chaetotaxy of the Head.

The chaetotaxy of the head of *C. nubeculosus* (figs. 4 and 5) closely resembles that of the terrestrial Ceratopogonid *Forcipomyia*, as described by Saunders (1924), and Saunders' terminology, with additions, is used here. Exclusive of the setae and sensillae on the mouth-parts there are 19 pairs of setae and sensory pits on the head of *C. nubeculosus*, and most of these can be homologized with those of *Forcipomyia*, which, however, has only 13 pairs. The frontal suture in *F. picea* Winnertz (fig. 6, *f. s.*), though much shortened, helps considerably in establishing the homologies.

In *F. picea* the sensilla "r" is situated between the eye and the frontal suture. In *C. nubeculosus* it is clearly represented by the sensilla also labelled "r." It is then clear that the long seta "p" of *F. picea* is represented in *C. nubeculosus* by two setae. On the dorsal side of the head there can be no doubt about the homologies of the setae "q," "t" and "x," although again a single seta, "x," in *F. picea* is represented in *C. nubeculosus* by a group of two setae. The sensilla "z" falls into the same pattern. On the lateral aspect of the head the seta "w" can be related in both cases from its position near the upper end of the sub-genal band; and the setae "u," "v" and "y" occur in the same downwardly curving arc which begins with "w." At the centre of this arc, as it were, in the lower lateral region of the sub-genal band in *F. picea* is the seta "o," and again in *C. nubeculosus* this is clearly represented by a group of two setae. The remaining seta "s" in *F. picea*, between the eye and the seta "u," is undoubtedly represented in *C. nubeculosus* by the pit with the tiny conical process, somewhat displaced anteriorly and dorsally. This is made more evident by the fact that in other species of *Culicoides* the tiny conical process is represented by a normal seta.



FIGS. 6-9.—(6) Lateral view of the head of the larva of *Forcipomyia picea* (after Saunders). *f.s.*, frontal or epicranial suture. (7) Lateral view of the anterior end of the head of *C. nubeculosus*. *ant.*, antenna; *c.s.*, club-shaped sensilla; *g.*, galea; *hypost.*, hypostomium; *l.*, lacinia; *mnd.*, mandible; *p.*, maxillary palp; *s.s.*, setiform sensilla; *st.*, stipes. (8) Antenna. (9) Anterior view of maxilla. Lettering as in fig. 7.

The sensillae in *C. nubeculosus* not represented in *Forcipomyia* are the pair of pits "j," each with a tiny conical process, behind each posterior arm of the epicranial suture; the pit "k" just in front of "s," the pit "m" between the setae "u" and "v," and the pit "n" just above the setae "o."

In some other species of *Culicoides* and of *Ceratopogon* some of the setae are divided so that up to 5 setae appear to arise from the same base. This phenomenon of divided or branching setae also occurs in the larvae of some mosquitoes.

2. The Labrum (figs. 7 and 11).

The labrum is a thick, rounded mass with membranous walls. There is no suture in any ordinary sense between it and the dorsal wall of the head, but only a sharp line of demarcation between the sclerotized capsule and the membranous labrum.

Anteriorly it bears four bulbous sensillae; antero-ventrally, four large thin-walled setae and two pairs of small setae in the mid-line; ventrally, a pair of small, recurved, sclerotized hooks; and latero-ventrally, in the plane of the maxilla, three curved and pointed sclerotized projections, like a trident, which, together with the ventral hooks, are the external ends of internal structures (figs. 12, 15 and 16, *labr. h., mess. f.*).

It may be inferred from the structure and musculature of the labrum that it is mobile to a small extent, but no movement has been observed.

3. The Antennae (figs. 7 and 8).

The antennae are in the normal position for what Thiennemann calls the *Ceratopogoninae vermiformes*. Saunders (1924, 1925) points out that *Forcipomyia*, *Thyridomyia* and *Apelma* form a series in which the antenna migrates forwards from a position mid-way along the head in *Forcipomyia*, through a point half-way between this and the labrum in *Thyridomyia* to a position above the base of the mandible in *Apelma*. So far as one can judge from his figures, the position of the antennae appears to be correlated with inclination of the head on the long axis of the body; in his figures of *Forcipomyia* the head is strongly inclined at an angle of about 80°; in *Thyridomyia* the angle is about 65°, and in *Apelma* the head is parallel to the long axis. In *Culicoides* the head is also very nearly parallel to the long axis and, perhaps consequently, the antennae are at the anterior end of the head, above the bases of the mandibles.

The antenna (fig. 8) has its base in a little hollow on the dorso-lateral border of the labrum. The mesal edge of this hollow bears the two small setae, "x." The base of the antenna is membranous and cushion-like. The second segment is also short and broad and bears on its dorso-lateral anterior surface two or three small papillae and a short two-segmented structure, while on the mesal surface there is a large cushion-like papilla. From a comparison with the larval antenna of a species of *Ceratopogon* in which the two-segmented structure has become elongate, it is evident that in *Culicoides nubeculosus* the antenna is morphologically four-segmented, with some sense organs on the second segment, and the large cushion-like papilla corresponds to the blade found in Chironomid larval antennae. The first segment or antennal base

corresponds to the so-called peduncle of some Chironomids, and, in this terminology, the antennae has three segments, the terminal fourth being wanting, as it occasionally is in Chironomids.

4. *The Mandibles* (figs. 7, 11 and 18).

The mandible is dark and heavily sclerotized, rather curved and blade-like in the distal third and pointed at its tip. On the inner side, about three-quarters of the length from base to tip there is a deep notch forming a tooth. The outer articulation is on the sclerotized ring (the subgenal band), round the anterior end of the head (fig. 16, *e. mnd.*) and the inner articulation on an internal sclerotization (fig. 16, *i. mnd.*). There is a seta at the base (shown only in fig. 18). The mandibles may be moved together or alternately and, because they are nearly parallel, their tips do not meet at any point.

5. *The Maxillae* (figs. 7, 9 and 11).

The maxilla is quite large. The dorsal edge of its base arises just ventral to the base of the mandible, runs anteriorly for a little way parallel to the long axis of the head, and then turns through a right angle to run ventrally almost to the ventral side of the labrum, where it turns again through a right-angle and disappears behind an anterior projection of the lateral wall of the head capsule, so that this area of the maxilla is roughly square. Half-way up, near the anterior border, there is a pair of papillae. On the ventral side of the antero-ventral corner there is a stubby segment which also bears a pair of papillae. This segment is obviously the palpus (figs. 7 and 9, *p.*) and the square area is probably the stipes (figs. 7 and 9, *st.*). It can be only a suggestion that the papillae on the stipes represent the galea (figs. 7 and 9, *g.*).

Mesad of, and posteriorly and slightly ventral to the stipes is a thin bilobed structure, with its lateral face slightly convex, bearing a single small seta and several sensillae. This is probably the lacinia (figs. 7 and 9, *l.*).

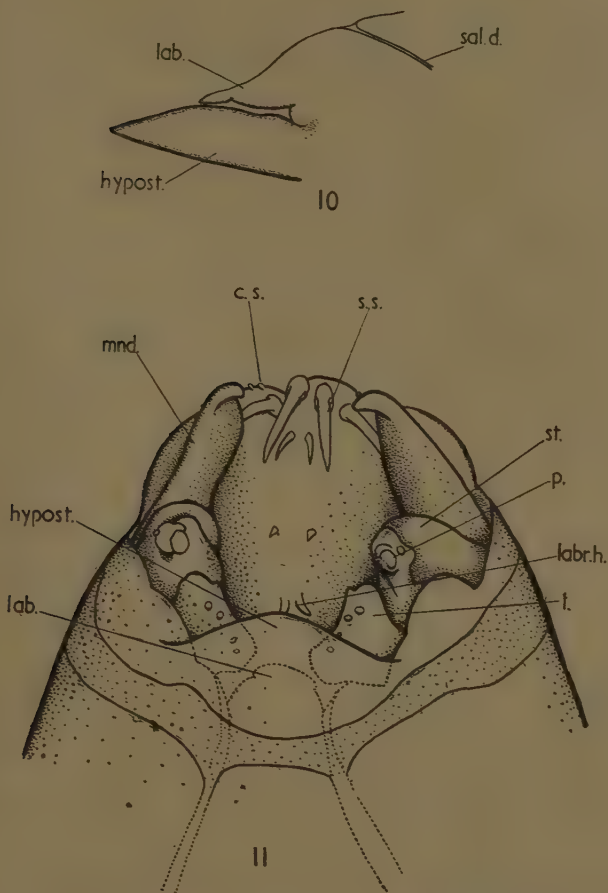
The mobility of the maxilla is a matter of inference from its structure and musculature rather than of observation.

The simple maxillary skeleton will be described in the section on internal sclerotized structures.

6. *The Labium* (figs. 10 and 11).

What appears at first sight to be the labium is a simple, smooth triangular extension of the ventral side of the head capsule, just reaching to the ventral part of the labrum and without any groove or line of demarcation between it and the ventral wall of the head capsule. Sagittal section, however, reveals that the dorsal wall of this extension (the ventral wall of the pre-oral cavity) is invaginated to form a pocket, the mouth of which is directed anteriorly. The walls of the pocket itself show some indications of segmentation, but the overlying ventral wall of the pre-oral cavity passes smoothly without trace of segmentation past the orifice of the salivary duct into the hypopharynx. Despite the simple nature of this region, there is little doubt that the structure formed by the dorsal wall of the pocket and the ventral wall of the pre-oral cavity overlying it is, in fact, the labium. The triangular extension of the head capsule is merely a secondary outgrowth of the capsule wall and may

well be described as the "hypostomium" (Anthon, 1943a). The supposed development of this "hypostomium" will be discussed in the section on morphology. In specimens treated with potash, viewed from below, the

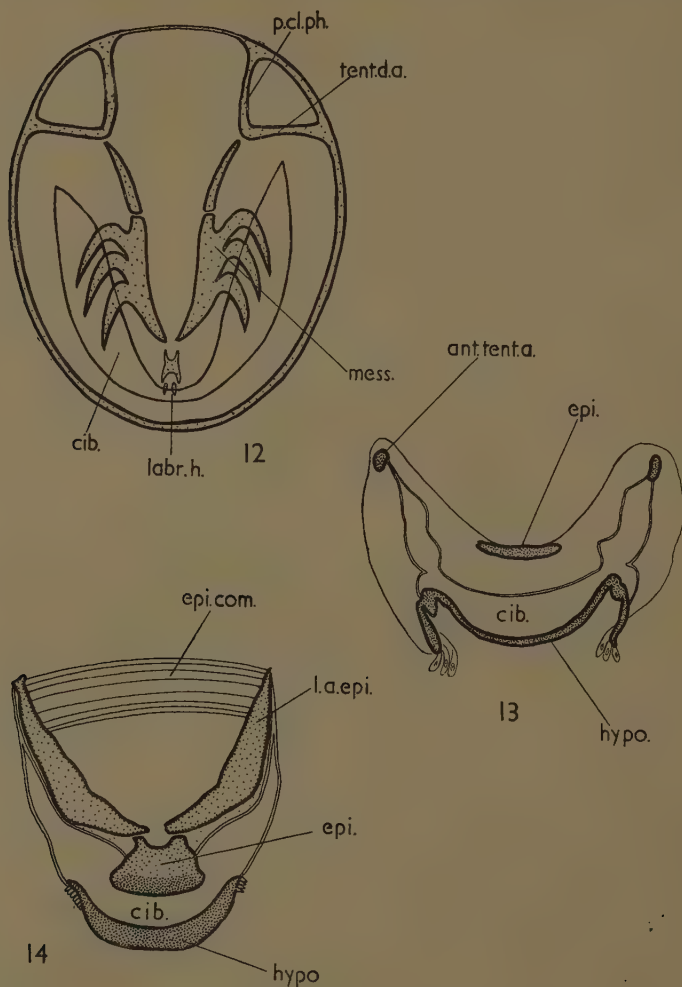


FIGS. 10, 11.—(10) Median longitudinal section through hypostomium and labium. *hypost.*, hypostomium; *lab.*, labium; *sal.d.*, salivary duct. (11) Ventral view of mouthparts. *labr.h.*, labral hooks. Other letters as in figs. 7 and 10.

labium proper is visible through the hypostomium as a broad structure with a curved anterior edge, behind which is a transverse suture. It appears to be without muscles and to be functionless. In view of this and of its reduced state, any attempt to establish homologies would be guesswork.

7. The Sclerotized Structures of the Head.

In figs. 4 and 5 complex structures are indicated surrounding the alimentary tract and occupying a central position in the head; these closely resemble the



FIGS. 12-14.—(12) Diagrammatic transverse section through the region of the messor. *cib.*, cibarium or pre-oral cavity; *labr.h.*, labral hooks; *mess.*, messor; *p.cl.ph.*, paraclypeal phragma; *tent.d.a.*, dorsal arm of tentorium. (13) Transverse section through the anterior region of the pharynx. *ant.tent.a.*, anterior arm of the tentorium; *cib.*, pre-oral cavity; *epi.*, epipharynx; *hypo.*, hypopharynx. (14) Transverse section through pharynx. *epi.com.*, compressor muscles of the epipharynx; *l.a.epi.*, lateral arm of the epipharynx. Other letters as in fig. 13.

structures shown in Saunders' figures of *Forcipomyia*. Other articulated structures occur within the mass of the labrum, in the region of the sub-genal band. The sub-genal band itself has internal processes of considerable morphological interest. A reconstruction of these structures is given in fig. 16, the capsule wall being absent except for a small strip joining the dorsal ends of the sub-genal band, and fig. 19 shows their relation to the alimentary tract.

From fig. 19 it will be seen that the alimentary tract curves upwards from its opening under the labrum to the central sclerotized structure, beyond which it then dilates to form the pharynx. The light area above the anterior portion of the tract represents an upward and outward extension of the left side. This is more clearly seen in figs. 12, 13 and 14, which represent cross-sections taken (a) in the region of the labrum, (b) just anterior to the centre of the head, and (c) in the region of the central sclerotized structure. From the muscles inserted upon it and from the nature of the sclerotizations this anterior region of the tract is to be regarded as the pre-oral cavity or cibarium. Anteriorly the cibarium is U-shaped, the inner walls being formed by the deep labrum, the lateral walls by the maxillae and the ventral wall by the labium and hypostomium. Posteriorly the arms of the cavity diverge, so that it becomes V shaped. The posterior end of this V-shaped region, where it dilates to become the pharynx, and where the central sclerotization occurs, is to be regarded as the morphological mouth, because of its relations to some of the muscles and to the frontal ganglion and the orifice of the salivary duct.

The existence of a central sclerotized structure in other CERATOPOGONIDAE has long been known and it has usually been referred to as the "hypopharynx." It will be shown in the section on morphology that this term is inapplicable, and here the sclerites of which the structure is made up will be referred to collectively as the "pharynges," a term which, without being quite appropriate, preserves a resemblance to the old term, but does not have its morphological implications. The component sclerites will be individually named.

The anterior sclerotizations inside the head are all either processes of, or are articulated to the "sub-genal band." This part of the capsule wall is to be homologized with Anthon's (1943a) "*sub-genal rand*" of the PHRYNEIDAE (= RHYPHIDAE; ANISOPODIDAE) and PSYCHODIDAE. I have interpreted the word "*rand*" as "*band*," this appearing to be the most appropriate here. It is not, as a sclerotized thickening, a complete ring, for in the dorsal region, between the antennae, it thins to the normal thickness of the head capsule. In fig. 16 this part of the capsule is shown joining the dorsal ends of the band.

The sub-genal band is not set squarely to the long axis of the head, but is tilted so that the ventral side is most posterior. It begins just mesad of the antenna on each side, and here it sends a process ventrally into the head, a plate to be homologized with the "paraclypeal phragma" of the Culicidae described by Cook (1944) (fig. 16, *p. cl. ph.*). At the same level there is a short posterior prolongation of the band in the capsule wall. Laterad of, or below the antenna there is a longer posterior prolongation in the capsule wall, and at the same point a plate extends inwards from the band to fuse with the paraclypeal phragma. This plate is the dorsal arm of the tentorium. Slightly below this, the anterior edge of the band has a slight indentation in which articulates the outer (posterior) condyle of the mandible (fig. 16, *e. mand.*). Below the articulation the band gives off antero-dorsally a broad, square-ended exten-

sion, reaching to the region of the antero-dorsal corner of the maxilla. Below this, the band curves smoothly downwards to the ventral side, where it forms part of the hypostomium. The ventral wall of the cibarium in this region is also strongly sclerotized and forms a downwardly curved arch, the lower ends of which fuse with the sub-genal band on each side of the hypostomium. From this line of union is given off posteriorly on each side a sclerotized rod which unites with and supports the hypopharynx.

The paraclypeal phragma is not a flat plate; its anterior edge curves out to meet the lateral wall of the labrum, just anterior to the base of the antenna. In transverse section, just posterior to the antenna, the paraclypeal phragma, the dorsal arm of the tentorium and that part of the sub-genal band between them together form roughly a sector of a circle, with the sub-genal band as circumference. The line of union of the paraclypeal phragma and the dorsal arm of the tentorium gives off posteriorly a sclerotized rod which runs along the upper edge of the lateral extension of the cibarium, and its posterior end is connected by a ligament to the upper end of the lateral sclerite of the pharynges (the suspensorial arm of the epipharynx). This rod is the anterior arm of the tentorium (fig. 16, *ant. tent. a.*).

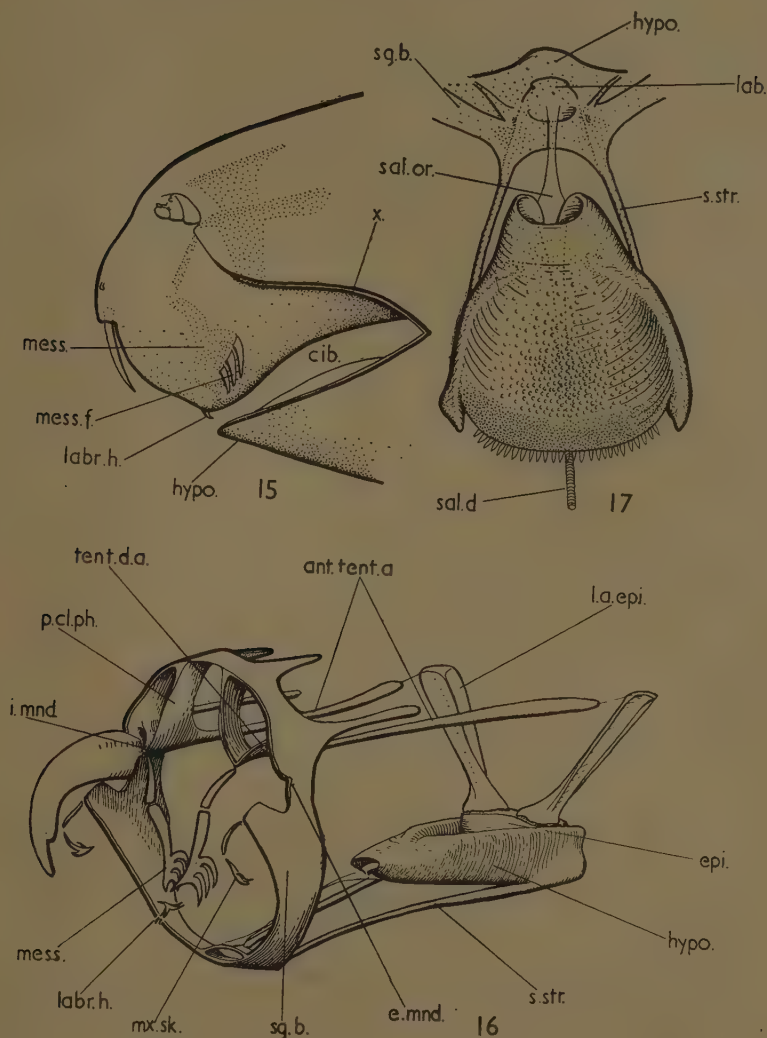
The inner (anterior) articulation of the mandible is on the line of union of the paraclypeal phragma and the dorsal arm of the tentorium, near its anterior end (fig. 16, *i. mnd.*).

Another structure also articulates with the anterior end of this line of union. This structure consists of two sclerites and is homologous with the "messor" of the CULICIDAE, described and so-called by Cook (1944), and originally called the "premandible" by Goetghebuer (1925). The upper sclerite of the messor connects dorsally with the line of union of the phragma and tentorial arm, and ventrally, at about half the depth of the labrum, with another more complex sclerite (fig. 16, *mess.*). This sclerite curves downwards towards the mid-line, and there, with its fellow of the other side, is linked by a complex median sclerite to a pair of tiny hooks, the tips of which emerge from the ventral side of the labrum (fig. 16, *labr. h.*). In its lower half the ventral sclerite of the messor gives off laterally and posteriorly a broad process which divides almost immediately into three recurved projections, together like a trident, the distal portions of which emerge from the latero-ventral wall of the labrum (fig. 15, *mess. f.*), in the region of the maxilla. The median sclerite, which links the messores with the labral hooks, consists of a small solid central portion and three pairs of pointed projections, one anteriorly to the messores, one ventrally to the labral hooks and the third posteriorly. On the posterior pair are inserted a pair of muscles, the labral compressor (fig. 19, *lab. com.*).

The antero-lateral, square-ended extension of the sub-genal band bears the point of articulation of the skeleton of the maxilla (fig. 16, *mx. sk.*). The maxillary skeleton consists of an upper, short, simple strut, which connects at its lower end with a sclerite having three curved pointed processes, one directed antero-laterally, another directed laterally and the third posteriorly. The posterior process has the maxillary muscle inserted upon it (fig. 20, *mx. sk., mx. m.*).

8. The Pharynges.

The pharynges are divisible roughly into two main parts, the one consisting of those elements which form the dorsal wall of the V-sectioned pre-oral cavity,



FIGS. 15-17.—(15) Lateral view of the anterior end of the head with the left mandible and maxilla and part of the wall of the pre-oral cavity removed. *cib.*, cibarium; *mess. f.*, messorial fork; *x.*, cut edge of wall. Other letters as in figs. 7 and 12. (16) Diagrammatic reconstruction of the skeletal structures of the head, the capsule being absent except for a strip joining the dorsal ends of the sub-genal band. *ant.tent.a.*, anterior arm of the tentorium; *e.mnd.*, external articulation of the left mandible; *epi.*, epipharynx; *hypo.*, hypopharynx; *i.mnd.*, internal articulation of right mandible; *labr.h.*, labral hooks; *la.epi.*, lateral arm of the epipharynx; *mess.*, messor; *mx.sk.*, skeleton of maxilla; *p.cl.ph.*, paraclypeal phragma; *sq.b.*, sub-genal band; *s.str.*, supporting struts of the hypopharynx; *tent.d.a.*, dorsal arm of the tentorium. (17) Dorsal view of the hypopharynx and its connections with the labial region. *hypost.*, hypostomium; *lab.*, labium; *sal.d.*, salivary duct; *sal.or.*, region in which the salivary duct opens; *sq.b.*, sub-genal band.

and the other of that single element which forms the floor and lower outer wall of the cavity. Essentially the single ventral element has the shape of the curved surface of that smaller part of a cone which has been divided by a plane parallel to its axis, the narrow end directed anteriorly and the concavity directed dorsally. This is the hypopharynx proper. Anteriorly a membranous extension of the narrow end is directed downwards to the labium. Half-way to this point occurs the conical opening of the salivary duct (fig. 19, *sal. or.*). Each side of the hypopharynx is reflected downwards, and posteriorly this reflected portion reaches a slightly greater depth than that reached by the central portion (fig. 16). The posterior end of the reflected portion is continued forward as the sclerotized rod which fuses with the sub-genal band in the labial region and thus supports the hypopharynx (fig. 16, *s. str.*).

The concavity or trough of the hypopharynx is nodular and the posterior margin is more heavily sclerotized than the rest (fig. 17).

The dorsal part of the pharynxes consists of a median element which normally sits in the trough of the hypopharynx, and of a pair of dorso-lateral arms abutting on and articulating with the median element. The median element itself is the epipharynx (figs. 13, 14, 16, 18, *epi.*, and fig. 35), and is a solid mass, about half as long as broad. Its ventral surface is curved so as to fit fairly closely into the trough of the hypopharynx; its dorsal and anterior surfaces are roughly plane and at right angles to each other, being approximately horizontal and vertical respectively. The posterior surface is recessed near the dorsal edge to receive the base of a pair of comb-like sclerites which project backwards in a horizontal plane and have two other median sclerites on their ventral face. Each sclerite of the pair of combs is roundedly triangular, with the apex anteriorly: the lateral edge is convex, the mesal edge concave and closely approaching its fellow of the other side in the mid line. The posterior edge of each sclerite is divided into 8–12 teeth, which are largest near the mid line, becoming smaller laterally. Occasionally the larger teeth are truncated, probably owing to their having been broken off or worn down in action.

On the ventral face of these sclerites, the “dorsal combs,” is a median sclerite, roughly triangular, the apex directed posteriorly. The homologue of this sclerite in other species of *Culicoides* will be referred to as the “second comb” in a work in preparation. Immediately anterior to this sclerite, and abutting on its anterior edge, is another sclerite, the “third comb,” which has its posterior edge practically straight and its anterior edge curved in an arc and fitting against the solid median block.

This is the type of structure found in most of the specimens of *C. nubeculosus* examined, and accords with the figure of the “hypopharynx” given by Mayer (1934). The details appear to be reasonably constant. Out of 17 specimens examined, 16 showed no great variation except in the number of teeth in the dorsal pair of combs, the range being from 8 to 12, with 10 as the commonest. A similar pattern was found in a specimen of *C. nubeculosus* taken at Dreghorn in Ayrshire by Edwards in 1922 [British Museum (Natural History) Collection].

In the exceptional specimen examined, however, the posterior edge of the second and third sclerites was produced into teeth; the second with 6–9 teeth on each side of a sharp median tooth; the third with 16–18 teeth. The

posterior edge of the median block was widely emarginate on each side of the mid line. The second and third sclerites overlap each other and thus it is necessary to dissect out the epipharynx and examine it from the ventral side with a $\frac{1}{12}$ oil-immersion objective in order to see all the teeth.

The difference between the two types is quite marked, and in the Dorset specimens there were no intermediate forms. In specimens from Achterawe, Inverness-shire, however, the third sclerite was produced into about 14 teeth, while all the other sclerites were similar to those of the common Dorset type. In a specimen of *C. riethi* Kieffer from the British Museum Collection, both the second and third sclerites are irregularly toothed and the postero-ventral

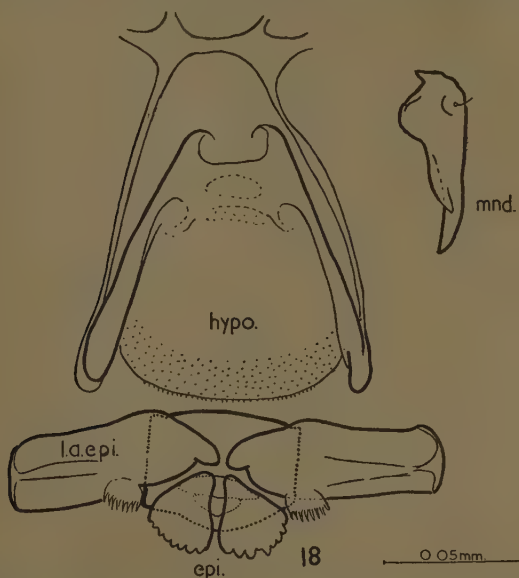


FIG. 18.—Outline drawings of the epipharynx, hypopharynx and mandible. *epi.*, epipharynx; *hypo.*, hypopharynx; *l.a.epi.*, lateral arm of epipharynx; *mnd.*, mandible.

edge of the median block has a number of wide, shallow indentations giving the appearance of about 6 broad smooth teeth. In this species, however, the size of the epipharynx is considerably less than that of *C. nubeculosus*.

The existence in the *C. nubeculosus* group of this series from smooth sclerites to definitely toothed sclerites is of some interest, since in most other species of *Culicoides* the second and third sclerites have well-developed teeth and the median block is reduced to a curved triangular plate, the "fourth comb," with its posterior edge toothed.

The lateral arms of the epipharynx (figs. 14 and 16, *l. a. epi.*) each have a long dorso-lateral portion and a shorter portion extending inwards along the dorsal surface of the epipharynx, so that their tips almost meet in the mid-line. The angle of the arm projects laterally beyond the edge of the epipharynx like

a heel. On the inner aspect of the arm a strengthening ridge runs from near the dorsal tip to the inner tip. From the dorsal tip of each arm is the membranous connection to the anterior arm of the tentorium.

On the posterior side of each arm, just dorsal to the angle, is a small anteriorly rounded sclerite with, as it appears in specimens treated in potash, its posterior edge frayed out into fine membranous fibres. In life these fibres are muscle attachments. The union of these sclerites with the arms is tenuous and transparent, but the sclerites remain in position after potashing, and as they transmit muscular tension to the arms the connection appears to be of considerable strength.

The point to be noticed about all these sclerotized structures of the head is that they are part of a single complex, which is bound together by the sub-genal band. It will be as well also to notice which parts are movable and which rigid. The mandibles and the maxillary skeletons are, of course, each movable as a whole; the messorial complex has four pairs of joints, one at the paraclypeal phragma connection, one halfway along the messor proper, one at the connection between messor and median sclerite and the last between the median sclerite and labral hooks. The arms of the epipharynx are slung from the posterior ends of the anterior arm of the tentorium and can swing antero-posteriorly; possibly they can also move laterally to a slight extent. The epipharynx itself is fixed to the arms. The hypopharynx appears to be rigidly attached to the labial part of the sub-genal band, but there is no doubt that in part it is movable, for, as will be seen, a pair of muscles is inserted upon it.

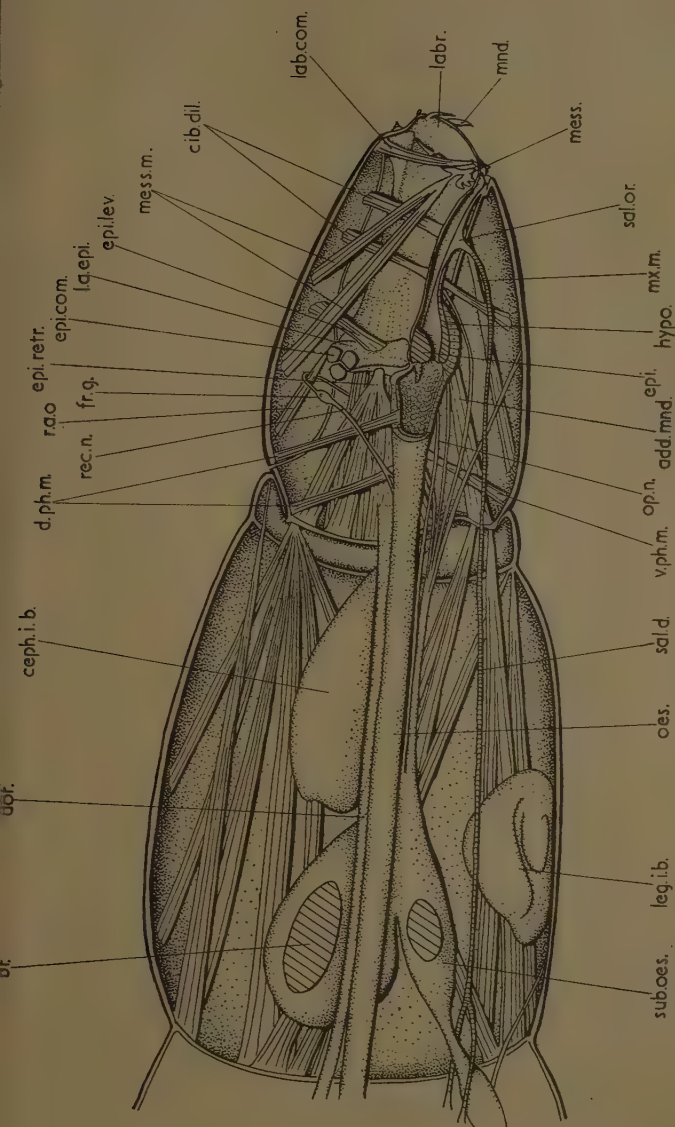
9. *The Musculature of the Head* (figs. 19, 20 and 21).

From the dorsal wall of the head capsule, in the plane of the sub-genal band, arises a very closely paired muscle which runs vertically downwards and is inserted on the median sclerite connecting the messors and the labral hooks. This is the labral compressor (fig. 19, *lab. com.*).

A pair of muscles is inserted on each messor near the origin of the trident. Each muscle passes dorsally and posteriorly to its origin on the capsule, the one slightly before and the other slightly beyond halfway along the head. These are the messorial muscles (figs. 19 and 21, *mess. m.*).

The abductor muscle (fig. 20, *abd. mnd.*) of the mandible spreads out in a broad fan from its insertion on the dorsal side of the base of the mandible to its origin along the lateral region of the collar. The adductor muscle (figs. 19 and 20, *add. mnd.*) of the mandible is single and takes its origin in the latero-ventral region of the collar. It should be noticed that there are two very curious points about the musculature of the mandible possibly related to the unusual plane of its movements. First, the origins of the muscles are reversed; ordinarily the abductor muscle takes its origin on the latero-ventral region of the post-occiput and the adductor on the lateral region. Second, the abductor is much larger than the adductor, which is again the reverse of the normal. The only reason which can be put forward for this is that more energy is required for abduction than adduction.

The maxillary muscle is inserted on the posterior end of the ventral strut of the skeleton, and takes its origin on the ventral posterior wall of the capsule anterior to the collar (figs. 19 and 20, *mx. m.*).

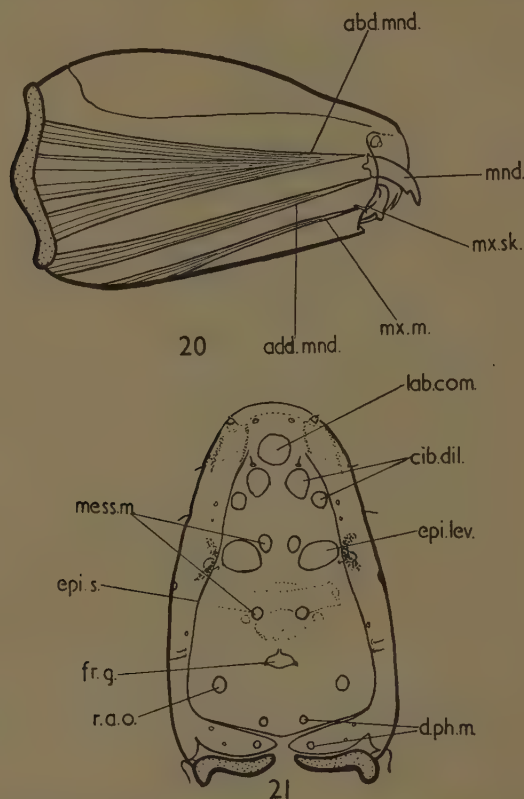


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FIG. 19.—The left half of the head and prothorax. *add.mnd.*, adductor muscle of the mandible; *aor.*, aorta; *br.*, brain; *ceph.i.b.*, cephalic imaginal bud; *cib.dil.*, dilator muscles of the cibarium; *d.ph.m.*, dorsal pharyngeal muscles; *epi.*, epipharynx; *epi.com.*, compressor muscles of the epipharynx; *epi.lev.*, levator muscle of the epipharynx; *epi.retr.*, retractor muscles of the epipharynx; *fr.g.*, frontal ganglion; *hypo.*, hypopharynx; *lab.com.*, compressor muscle of the labrum; *labr.*, labrum; *lq.epi.*, lateral arm of the epipharynx; *leg.i.b.*, leg imaginal bud; *mess.*, mesor; *mess.m.*, mesorial muscles; *mnd.*, mandible; *mx.m.*, maxillary muscle; *oes.*, oesophagus; *op.n.*, optic nerve; *r.a.o.*, "retractor muscle of the mouth angle"; *rec.n.*, recurrent nerve; *s.d.*, salivary duct; *s.d.or.*, orifice of salivary duct; *sub.oes.*, sub-oesophageal ganglion; *v.ph.m.*, ventral pharyngeal muscle. The abductor muscle of the mandible is seen behind the retractor of the epipharynx, just posterior to the lateral arm.

No antennal muscle is visible; presumably it takes its origin, if it is present, on the dorsal arm of the tentorium as normally.

There are two pairs of dilators of the cibarium, the anterior pair the stouter and originating on the capsule near the mid-line, while each muscle of the posterior pair originates just on the mesal side of the ecdysial suture (figs. 19 and 21, *cib. dil.*).



Figs. 20, 21.—(20) Lateral view of the head to show the muscles of the mandible and maxilla. *abd.mnd.*, abductor muscle of the mandible; *add.mnd.*, adductor muscle of the mandible; *mnd.*, mandible; *mx.m.*, maxillary muscle; *mx.sk.*, skeleton of maxilla. (21) Dorsal view of the head to show the origin of the muscles. *cib.dil.*, cibarial dilators; *d.ph.m.*, dorsal pharyngeal muscles; *epi.lev.*, levator of the epipharynx; *epi.s.*, epicranial suture; *fr.g.*, frontal ganglion; *lab.com.*, labral compressor; *mess.m.*, messorial muscles; *r.a.o.*, retractor of the mouth angle.

A pair of muscles is inserted on the anterior membranous part of the hypopharynx, posterior to the opening of the salivary duct, and originates on the ventral wall of the head. This is obviously the retractor muscle of the hypopharynx which, in the generalized insect head, has its origin on the tentorium (fig. 19).

There are three sets of muscles inserted on the arms of the epipharynx. First, a close group of three muscle bands connecting their dorsal ends (fig. 19, *epi. com.*). Second, a muscle inserted on each antero-mesal face near the ventral end and passing antero-dorsally to originate on the clypeus (figs. 19 and 21, *epi. lev.*). Neither of these groups can be homologized with any muscles in the generalized insect head, unless the second is to be regarded as the buccal dilator, in which case "epipharynx" is a misnomer for the sclerite I have so named, for it is then within the morphological mouth. The question may be left open, but with this reservation I shall continue to use the term epipharynx. These muscles may be called the compressor of the epipharynx and the levator of the epipharynx respectively.

The third muscle (figs. 19 and 21, *r. a. o.*) of the epipharyngeal arms is inserted on the dorsal end of the arm, and runs postero-dorsally to originate on the posterior region of the clypeus, near the ecdysial suture. The loop of the recurrent nerve passes over this muscle on its way to the frontal ganglion. The derivation of this muscle is clear; it represents the retractor of the mouth angle of the generalized insect head which is ordinarily inserted on the suspensorium of the hypopharynx.

On the small sclerite attached to the lower posterior edge of each arm is inserted a group of muscles fanning out to their origin on the lateral region of the collar mesad of the abductor muscles of the mandible. This is a very powerful group and may be called the retractor of the epipharynx (*epi. retr.*).

Posterior to the pharynxes the gut has two pairs of dorsal muscles and a single pair of ventral muscles. The ventral muscles (*v. ph. m.*) take their origin on the head capsule just anterior to the collar and near the mid-line. The anterior pair of dorsal muscles originate near the dorsal mid-line just anterior to the ecdysial suture (fig. 21, *d. ph. m.*). The posterior dorsal pair originate posteriorly to the lateral arms of the suture and are separated by the short coronal stem. Of these two dorsal pairs, the anterior pair belongs to the first set of pharyngeal dilators and the posterior pair to the second set, each pair representing what is often two pairs in the generalized insect head.

10. Feeding Movements.

I have never been able to observe feeding in the larvae of any species of *Culicoides*. They settle down quietly in an observation vessel only when there is enough substrate—mud or cotton-wool for instance—for them to bury themselves and then they are almost impossible to observe continuously. Without the minimum amount of substrate they are restless and are continually on the move. Species of *Tetrphora* (= *Dasyhelea*), however, are extremely sluggish and may, so to speak, be fed by hand, by pushing filaments of algae or detritus within reach of the mouth. The structure of the mouth-parts and the pharynxes of *C. nubeculosus* in particular, and those of other species of *Culicoides* to a lesser extent, so closely resemble those of *Tetrphora* that in all probability the method of feeding is also similar.

In *Tetrphora* the mandibles, either independently or together, make scratching movements at whatever is offered, so that small pieces are detached and pushed into the pre-oral cavity, whence they are prevented from escaping by the gratings of the messorial forks. The fragments are then drawn back by backwards and forwards piston movements of the epipharynx into the

region of the hollow of the hypopharynx, where they are subjected to grinding and stamping movements of the epipharynx. By the time they have been triturated the fragments have formed a bolus and the whole epipharynx is then drawn back so as to pass the bolus into the oesophagus, down which it slips smoothly until it reaches the ventricular valve, where there is usually a slight check before it passes into the mid-gut.

It is very probable that on mud-substrate the sclerotized anterior edge of the hypostomium is able to act as a plough.

It has not been possible to determine the precise relation between the movements of the mandibles and those of the messorial forks. The mandibles, in their backwards movements, have been observed to pass the forks, and in preserved specimens they are often found adducted well behind the forks. It may be suggested that movement of the mandibles in this direction is made without difficulty, but that in forward movements the mandibles are caught by the forks and are thus scraped free from adhering fragments. This extra effort involved in abduction might be responsible for the greater size of the abductor muscles compared with the adductor muscles.

11. *The Nervous System of the Head and Prothorax.*

The brain lies in the posterior half of the prothorax. The division between the two supra-oesophageal ganglia is well marked in each case. None of the cranial nerves is given off from the supra-oesophageal ganglia directly; instead, all of them appear to stem from the sub-oesophageal ganglia in the anterior region of their union with the circum-oesophageal connectives. The optic nerve (fig. 19, *op. n.*) arises alone in this region and proceeds immediately below the gut to a point just anterior to the ventral pharyngeal muscles, when it turns dorso-laterally to the eye.

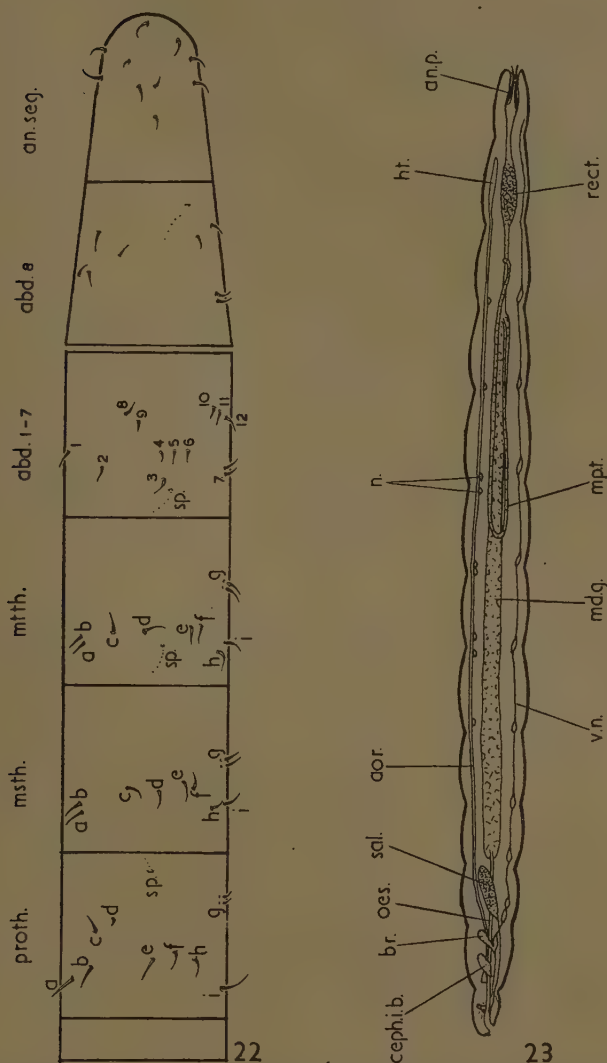
For the rest of the obvious cranial nerves the sub-oesophageal ganglion of each side tapers out anteriorly into a long trunk, which gives off a ventral branch in the anterior part of the prothorax, and later, just posterior to the foramen magnum, divides into three branches. The first ventral nerve supplies the anterior ventral wall of the head. The most dorsal branch of the main trunk is the frontal connective which, just posteriorly to the ventral pharyngeal muscle, diverges from the mid-line and passes antero-dorsally to recurve over the "retractor of the mouth angle" near its insertion on the suspensory arm of the epipharynx. In the mid-line the nerve of each side fuses with its fellow in the frontal ganglion (fig. 19, *fr. g.*), which thus remains in its primitive position just behind the mouth, although the brain has been withdrawn into the prothorax. From the frontal ganglion the single recurrent nerve (fig. 19, *rec. n.*) is given off posteriorly and reaches the gut in the region of the posterior pharyngeal dilator, where it gives off a short branch and then runs back along the dorsal wall of the gut, beneath the aorta.

The remaining two nerves supply the antennae and the setiform sensillae of the labrum.

The other cranial nerves are too minute for clear observation.

12. *The Sense Organs of the Head.*

The Eye.—The eye occupies a dorso-lateral position, laterad of the ecdysial suture and slightly anterior to the halfway point. It consists of a densely



FIGS. 22, 23.—(22) Setal diagram of lateral view of thorax and abdomen. *sp.*, spiracle. The lettering of the thoracic setae corresponds to that of *Forcipomyia*, but the abdominal setae do not correspond closely and are therefore numbered. (23) Internal structure of the larva. *an.p.*, anal papillae; *aor.*, aorta; *br.*, brain; *ceph.b.*, cephalic imaginal bud; *ht.*, heart; *md.g.*, mid-gut; *mpt.*, malpighian tube; *n.*, nephrocytes; *oes.*, oesophagus; *rect.*, rectum; *sal.*, salivary gland; *v.n.*, ventral nerve cord.

granular, pigmented, bilobed or bean-shaped mass, with the pigment granules less densely packed towards the edges, the total length being about 60 microns. Within the laterally directed hollow is a spheroidal lens. Posteriorly the pigment granules often thin out into a tail along the optic nerve, the course of which they thus mark for a greater or lesser extent from specimen to specimen. The granules stain deeply and the lens slightly with methylene blue.

Sensillae.—There are several types of sensillae on the head, the most remarkable being those of the anterior face of the labrum. These (figs. 7 and 11, c. s.), of which there are two set transversely closely together on each side of the mid-line, are small and club-shaped, with thin walls, drooping slightly on their short, slender stems. I am not aware that similar organs have been described elsewhere.

The most prominent are the large setiform organs (figs. 7 and 11, s. s.) set transversely across the labrum just below the club-shaped organs, the mesal pair being slightly the larger. They are thin-walled and their bases are invaginated. From their position and size it might almost be thought that their function was mechanical; but from the thinness of their walls and the size of their nerve supply, which is considerable, it is clear that they are sensory organs.

The other sensillae are of the usual types. There are four pairs of basiconic organs, and four pairs of apparently simple shallow pits. Their positions have already been indicated in the section on the chaetotaxy of the head.

The Thorax and Abdomen of the Larva.

1. *The Cuticle.*

The whole cuticle, of the head as well as that of the body, is smooth, shining and hydrophobe, so that if the larva is lifted out of the water in which it is swimming and then replaced, it occasionally has difficulty in breaking through the surface film.

The outer layer of the cuticle is not completely intact, for if the larva is placed in a 0.005 per cent. solution of ammoniacal silver nitrate for twenty minutes, by which time the larva is immobilized, and then examined, the cuticle is found to be stained, particularly on the ventral side, with many small brown circular patches, which are sometimes so close as to run together. According to Wigglesworth (1945) such staining is due to the reduction of the silver nitrate by some constituents of the cuticle, and is made possible by abrasion of the epicuticle, leaving the rest of the cuticle exposed. In the present case the greater concentration of spots on the ventral side makes this explanation probable, although the circular shape of the spots is not easy to explain. Subsequent treatment with chloroform obviously alters the surface, for it becomes sticky, but the protective layer is not removed, apparently, for no further staining with silver nitrate takes place.

2. *The Neck.*

The neck is part of the prothorax, for although a few muscles are inserted on the "inter-segment" between prothorax and neck, there are no muscles belonging peculiarly to the neck. There are no setae whatever on it. The head may occasionally be retracted into it as far as the anterior end of the coronal suture.

3. Chaetotaxy.

All the setae of the body are smaller than the principal setae of the head, and the setae of the abdomen are smaller than those of the thorax (fig. 22). The chaetotaxy of the thorax is as closely related to that of *Forcipomyia* as is that of the head. In the mesothorax of *C. nubeculosus* the setae are small and simple, and all can be homologized with those of *Forcipomyia* with the exception of two setae found in the antero-ventral region which are not represented in *Forcipomyia*. The letters used by Saunders (1924) for the thoracic setae of *Forcipomyia* have been applied to the homologous setae in *C. nubeculosus*; the two additional setae in *C. nubeculosus* have been labelled "h" and "i."

The homologies in the chaetotaxy of the abdomen are not easily traced, for while there is a close resemblance between thoracic and abdominal chaetotaxy in *Forcipomyia*, in *C. nubeculosus* the relationship is obscure. Because of this lack of correspondence the abdominal setae of *C. nubeculosus* have been numbered so as not to be confused with the lettered setae of *Forcipomyia*. The chaetotaxy of the eighth abdominal segment is unlike that of any of the others and the setae are fewer. This discrepancy is not removed by regarding the eighth and anal segments as morphologically one.

A group of setae which are very clearly homologous in the thoraces of the two genera are those which, according to Keilin (1921), represent the vestigial sensory organs of the legs. In *C. nubeculosus* these appear in the ventro-lateral region of each segment of the thorax (fig. 22, g), and consist of a pair of small setae set closely together immediately below a pair of small sensillae also set closely together.

The posterior setae of the ninth segment are rather larger than those of the rest of the body and most of them are recurved, but their character is essentially the same as that of the others, in that they are pale and thin. In this, *Culicoides* differs from many of the other genera of the CERATOPOGONIDAE, where there are additional strong, black anal setae. However, the absence of these particular setae is not a feature peculiar to *Culicoides*, for in at least one species of *Ceratopogon* and of *Stilobezzia* all the anal setae are pale and thin.

4. The Spiracles (fig. 24).

The spiracles are not readily seen, partly because of their small size—those of the abdomen are about 4.5 microns in diameter—and partly because of their lack of marked pigmentation. The pro- and meta-thoracic spiracles have no close relation to a seta, but those of the first seven abdominal segments are each situated just anterior to the seta "3" (fig. 22). That of the eighth segment is in the posterior region of the segment and, like the thoracic spiracles, has no close relation to any seta.

The prothoracic spiracle is a simple elongate ellipse. The metathoracic spiracle has the same simple shape, but also has a few minute refractile granules within the margin. The abdominal spiracles are more complex and each consists of four components—a large anterior ring and two smaller rings of equal size immediately posterior and a much smaller ring in the interstice formed by the other three. The diameter of 4.5 microns of this complex makes it impracticable to resolve it further.

5: The Anal Papillae.

Like many other Nematoceran larvae *C. nubeculosus* has a pair of anal processes, of the type usually known as blood gills, each of which is subdivided into four lobes (fig. 25). They have their bases just within the anus, and can be withdrawn entirely into the anus. In the retracted state the papillae are not entirely exposed to the lumen of the rectum, but the base of each occupies a special thin-walled pouch derived from the wall of the rectum. Fig. 26 shows a section of this region where the retracted papillae are within their pouches.

The papillae are compressed laterally, so that viewed from above they appear almost like a pair of thick straight setae. The walls are thin, but because of the lateral compression the volume of the lumen is not large. There is no special concentration of tracheae in this region, nor does there appear to be any specially directed flow of blood to the papillae, so far as can be seen on examining the living larva.

It has already been shown by Thorpe (1933) and by Wigglesworth (1933) that no special respiratory function is attached to the very similar organs in aquatic larvae, and the inadequate means in *Culicoides* for transporting any oxygen taken up by the papillae lends support to the view that they do not have any such function here.

It has also been shown by Koch (1938) and Wigglesworth (1938) that the anal papillae in *CULICIDAE* are osmo-regulatory, actively absorbing chloride from the medium, and varying inversely in size with the salt content of the medium. Koch also points out that such organs are selectively stained by silver nitrate by the precipitation of an insoluble silver salt and its subsequent blackening on exposure to light. Krogh (1939) adds the warning that although silver-absorbing cells are prominent in the phyllopod *Branchipus*, he did not find any evidence of chloride absorption.

The anal papillae of *C. nubeculosus* are also stained by silver nitrate, but here the colour is not black, but a fine red with a slight brownish tinge, which indicates exceedingly fine dispersion of the silver particles, and possibly an active reduction by the organism rather than simple reduction of silver chloride by light. The effect of silver nitrate as a poison is also interesting; a 0.025 per cent. silver nitrate solution kills a larva in a little more than ten minutes, whereas urethane in large quantity has little effect after an hour, owing, no doubt, to the larger size of its molecule.

6. The Alimentary Tract.

The fore gut (figs. 19 and 23, oes.).—The buccal cavity has already been described in the account of the head, and only two points about the pharyngeal region remain to be mentioned. The lateral ventral borders of the hypopharynx are provided with a row of deep columnar cells which are quite unlike those of the pharynx. The pharynx itself, immediately posterior to the pharynxes, has a dorsal dilatation, which probably serves to accommodate the epipharynx in a backward swing and also provides scope for its forward swing.

The oesophagus, which may be assumed to begin posterior to the pharyngeal dilatation, is a thin-walled, narrow tube provided with circular muscles and leading directly to the ventricular valve in the anterior part of the meta-thorax.

The mid gut (fig. 23, *md. g.*).—At the ventricular valve the gut swells out to about five times the diameter of the oesophagus, and continues at this size or slightly less as far as the region of the anterior end of the seventh abdominal segment. The valve is very like that of *Forcipomyia* as described by Saunders (1924), and consists of an extension of the oesophagus into the mid gut. The walls of the mid gut are thick and are composed of deep columnar cells.

The hind gut (fig. 23, *rect.*).—The hind gut consists of four well-marked parts. In the anterior region of the seventh abdominal segment the mid gut contracts suddenly, so as almost to give the appearance of a valve, to form a narrow thin-walled tube much like that of the oesophagus. This occupies the length of the seventh segment and is then continued as a much wider tube, the walls of which are made up of large cells with obvious nuclei. Although this part of the hind gut is thick, the cells are so large that the lumen remains small. In the posterior region of the eighth segment the gut is continued into the last segment as a tube with much the same sized lumen, but with walls of smaller cells of columnar epithelium. This ends in a short bulbous section with large cells forming the walls from which the anal papillae arise. It is attached to the walls of the segment by retractor muscles. Finally, there is what might be called a post-anal cavity, formed when the rectum is retracted, and in which the anal papillae lie.

7. *The Malpighian Tubules* (fig. 23, *mp. t.*).

There are only two Malpighian tubules in *C. nubeculosus*, unlike *Forcipomyia*, where there are three, according to Saunders. They arise at the junction of the hind gut and mid gut and pursue a straight course anteriorly to the fourth segment, where they loop back and terminate in the seventh segment.

8. *The Salivary Glands* (fig. 23, *sal.*).

The salivary glands are large elongate organs occupying the greater part of the mesothorax, extending slightly into the metathorax and lying along the posterior part of the oesophagus. The walls are composed mostly of small cells, but scattered among these are a number of large cells with clear cytoplasm and large nuclei. Their ducts, thin-walled and ringed like tracheae, run forward to join in the mid-line in the region of the sub-oesophageal and first thoracic ganglia connectives. From thence the common duct continues in a straight course to open on the membranous anterior part of the hypopharynx (fig. 19).

9. *The Nervous System* (fig. 23, *br.*; *v. n.*).

The central nervous system consists of a large bilobed brain and sub-oesophageal ganglia situated in the posterior region of the prothorax, and followed immediately by the ganglia of the first thoracic segment lying in the anterior region of the mesothorax and the mesothoracic ganglia lying in the middle of the segment, and then by the ganglia of the metathorax and seven abdominal ganglia, each lying in the extreme anterior region of the segment to which it belongs.

The cephalic nervous system has already been described in the account of the head.

The ganglia of the ventral chain are rather elongate and taper smoothly into the connectives. The last pair of ganglia, although they represent the fused ganglia of the seventh and eighth abdominal segments, are no larger than the others. They give off a pair of long nerves reaching to the end of the anal segment. Each pair of ganglia gives off a pair of nerves passing backwards to the ventral region of its segment. Finer nerves are not visible with ordinary techniques.

The main part of the sympathetic system has been described in the account of the head. The recurrent nerve is not visible by ordinary methods after it has reached the dorsal surface of the oesophagus and no other parts of the system have been seen.

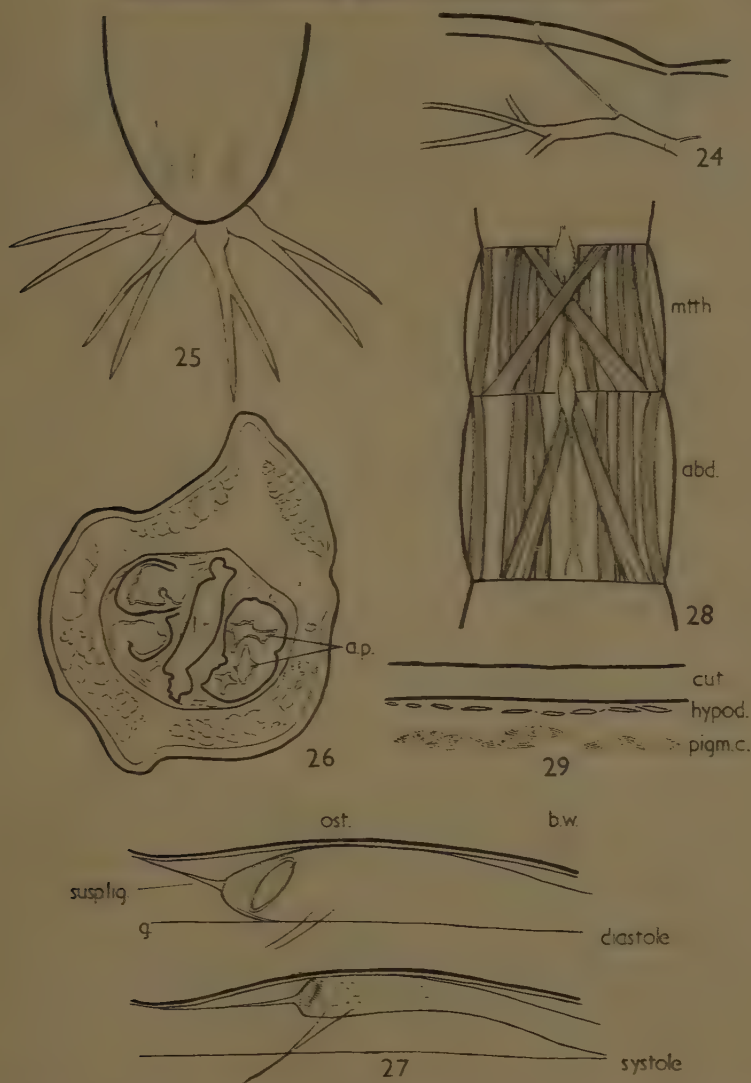
10. *The Heart and the Aorta* (fig. 23, *ht.*, *aor.*; fig. 27).

The heart and the aorta together form a long tube running from near the posterior end of the eighth segment to just within the head. At the posterior end the tube is bulbous and contractile, so that this region may be regarded as the heart, and passes insensibly into the narrow tube of the aorta, which remains the same diameter throughout its length until it reaches the head, where it expands into a funnel and so ends.

The dorsal surface of the heart is applied to the body wall and partly attached to it. A suspensory ligament connects its hind tip to the mid-dorsal line between the eighth and ninth segments, and another ligament attaches each side to the lateral body wall. On each side, between the posterior tip and the lateral suspensory ligament is a large ostium with definite lips. The inner wall of the heart in the posterior region is smooth, but towards the anterior end of the eighth segment it acquires irregularly spaced clumps of cells, which are seen for only a short distance along the aorta.

It has already been mentioned that pigment and fat body are largely absent from the eighth segment and the action of the heart can therefore be fairly readily seen. In diastole the heart occupies the whole of the vertical space between the gut and the dorsal body wall, the lips of the ostia are relaxed and the ostia themselves are widely open, and the wall of the heart is smooth. In systole the whole organ contracts against the tension of the elastic suspensory ligaments, the lips of the ostia contract and close their orifices, the wall becomes longitudinally wrinkled and the heart comes to lie close to the dorsal wall of the segment, leaving a space between itself and the dorsal wall of the gut. A wave of contraction passes forwards from the heart along the aorta and dies away in the region of the sixth segment. In its later stages this wave is undoubtedly passive and is due to the pressure wave in the blood, but at what point the active muscular contraction ceases is difficult if not impossible to say. The active contraction of the lips of the ostia as part of systole effectively prevents all but a trace of regurgitation. As might be expected, the heart rate varies considerably with the condition and circumstances of the larva, but in a larva lying quiescent under a coverslip for some time a common rate found was thirty beats per minute, although in one third instar larva a rate of 85 per minute was observed.

The blood is mostly a clear fluid, but it contains a fair number of particles consisting of single cells and clumps of two or three cells to the number of one to three particles passing into the heart with each beat.



FIGS. 24-29.—(24) Vestigial spiracle of prothorax from above, to show connection to trachea. (25) Lateral view of extruded anal papillae, somewhat displaced by pressure on the anal segment. (26) Transverse section through the anal segment to show the roots of the anal papillae separated from the rectum. *a.p.*, anal papillae of one side; *l.r.*, lumen of rectum. (27) Lateral view of the heart in diastole and systole. *b.w.*, body wall; *g.*, dorsal wall of gut; *ost.*, ostium; *susp.liq.*, suspensory ligament. (28) Dorsal view of the musculature in the ventral region of the metathorax and first abdominal segment. (29) Longitudinal section through the dorsal wall of the thorax showing pigment layer. *cut.*, cuticle; *hypod.*, hypodermis; *pigm.c.*, pigment cells.

There are paired groups of cells attached to the dorsal vessel at the anterior and posterior ends of the abdominal segments which the vessel traverses, except the first, where there are none, and the eighth, where there is only the anterior group (fig. 23, *neph.*). It is suspected that these are the nephrocytes, which in *Forcipomyia* occur in a similar position, but only in some cases were they stained on injection of ammonia carmine so that their nature must be left undetermined. The question is discussed in the next section.

11. The Nephrocytes (fig. 23, *n.*).

The detection of the nephrocytes in the larva of *C. nubeculosus* proved impracticable. Almost by definition the nephrocytes are groups of cells which are detected by *intra-vitam* staining; but using the technique adopted to inject ammonia carmine it was found impossible to keep larvae alive for the length of time necessary for clear staining. (Puri (1916) recommends thirty hours after injection as a minimum to be taken for *Cimex* before examining.) The staining obtained varied from specimen to specimen; some showed particulate staining of the wall of the rectum, others showed bright staining of small clumps of cells in the fat body, and others showed staining of the paired groups of cells applied to the dorsal vessel in each segment. All, however, showed brightly stained clumps of a few cells floating more or less freely in the body cavity and homogeneously stained diffuse strands encircling the body, except for the mid-dorsal and ventral regions, in each abdominal segment. Of all these, the only groups which would have been regarded, without staining, as probably nephrocytes are the paired groups attached to the dorsal vessel, and these, as has been said, took up the stain in only some cases. The question of the identity of the nephrocytes must therefore be left open.

12. The Tracheal System.

The tracheal system of *C. nubeculosus* closely resembles that of *Forcipomyia*. There are two main trunks running the length of the body in the dorso-lateral region and there are no functional spiracles. Each trunk gives off a lateral branch in each segment supplying the ventral region, and again in each segment a transverse branch connects the two trunks. There is a particularly conspicuous transverse connective in the anterior region of the mesothorax additional to the usual one. In the prothorax each trunk divides into two, and the mesal branch of each joins with its fellow in the mid-dorsal line to form a common trunk running into the head and ramifying there. Shortly after leaving the main trunk the mesal branch itself gives off a branch which breaks up and ramifies in the region of the brain. The lateral branches incline ventrally and converge to enter the head in the latero-ventral region.

There are no special plexuses in the region of the heart, and in the last segment the trunks taper off into tracheae without sending in special branches to the anal "gills."

The absence of functional spiracles is not confined to the CERATOPOGONIDAE among Dipteran larvae. According to Keilin (1944) the spiracles are also non-functional in BLEPHAROCERIDAE, CHIRONOMIDAE, SIMULIDAE, and in the genera *Chaoborus* (CULICIDAE), *Ceroplatus* (MYCETOPHILIDAE) and *Antocha* (TIPULIDAE).

This condition is therefore ordinarily correlated with aquatic life, and when it is present in terrestrial forms, e.g., *Camptocladius* and *Forcipomyia*, the terrestrial habit is assumed to have been secondarily developed.

The vestigial spiracles have already been mentioned. A pair is present in the pro- and metathorax and in each of the first eight abdominal segments. Each spiracle is connected to the lateral branch of the main trunk by a thin twisted ribbon-like tube. In the prothorax this connection arises near the inter-segmental junction with the mesothorax and passes anteriorly to the spiracle. In the metathorax the connection also arises near the junction with the mesothorax, but in this case the connection passes posteriorly to the spiracle. In the abdomen the connection also arises at the anterior end of each segment and passes backwards to the spiracle.

This accords with what Keilin (1944) has to say on the subject: ". . . the spiracles were originally intersegmental. From this it is easy to assume that the pro-meso-thoracic spiracle migrated forwards on to the prothorax and that the meso-meta-thoracic migrated backwards on to the metathorax; in addition, that the more posterior spiracles migrated backwards on to the segment immediately behind each."

At ecdysis the tracheae appear to divide into sections, and each section is withdrawn through the new spiracle by the connection to the old spiracle.

13. *The Fat Body.*

The fat body is prominent in all species of *Culicoides*, and often has a characteristic pattern which serves to distinguish the species.

In *C. nubeculosus* the bulk of the fat body is comprised in two broad lateral strips extending for most of the length of the abdomen, and in two narrow bands in the dorsum of the abdomen each running along the mesal side of one tracheal trunk. It is unpigmented.

When the living larva is examined with polarized light a curious twinkling appearance in the fat body is often seen. This seems to be due to the presence in individual cells of the fat body of minute motile particles which either alternate very rapidly between double and single refraction or by being present in depth cancel out each others' bi-refringency. If the cell is burst the expelled contents continue to exhibit the same phenomenon. Very probably these particles are symbionts of the type found in special bodies in *Tetrastoma* (= *Dasyhelea*) *obscura* by Keilin (1921). Keilin described these as bacteria: cocci, occurring in the fat body among others places, have been described in *Culicoides sanguisuga* (= *obsoletus*) by Hertig and Wolbach (1924) (quoted by Steinhaus, 1946). Bi-refringency of these organisms does not seem to have been observed.

14. *The Musculature.*

The muscles show up well with polarized light, not only in the living larva, but also in balsam mounts. In mounting media containing phenol, however, they do not show up at all.

The prothoracic pseudopod is present only in the first instar so that in the mature larva the musculature of the prothorax is relatively simple (fig. 19). The principal muscles of the segment proper are longitudinal, but one muscle.

on each side runs diagonally upwards from its insertion on the posterior edge of the collar to its origin on the upper lateral posterior border of the prothorax. The muscles inserted on the dorso- and ventro-lateral regions of the post-occipital ridge of the head are mostly longitudinal, but from the dorso-lateral insertion some pass to the dorsum of the prothorax while others pass to the ventro-lateral posterior region of the prothorax; and from the ventro-lateral insertion a pair of the muscles attached there run to the upper lateral region of the posterior end of the prothorax. This musculature accounts for the great independent mobility of the head.

The muscles of the mesothorax are longitudinal, except for a single muscle which runs forwards from the upper lateral to the lower lateral end of the segment on each side.

In the metathorax (fig. 28) there is a muscle chiasma in the ventrum in addition to the mesothoracic type of musculature. This consists of a pair of muscle bands, each of which is inserted on one side of the anterior end of the segment in the ventro-lateral region and passes across to the opposite ventro-lateral region of the posterior end. The crossover takes place about the middle of the segment.

In each of the abdominal segments but the last there is an apodeme in the mid-dorsal and in the mid-ventral line invaginated from the wall of the anterior "inter-segment." On each of these apodemes a pair of muscles is inserted. The muscles of each pair diverge posteriorly and take their origins at the posterior end of the segment in the dorso-lateral regions in the case of the dorsal pair and in the ventro-lateral regions in the case of the ventral pair (fig. 28).

These diagonal muscles are very probably concerned in the production of the rapid wriggling movement which appears to be peculiar to the CERATOPOGONIDAE.

In the terminal segment are the retractor muscles of the anal papillae.

There are no transverse or verticle muscles of normal type in any segment. In the mid-lateral region of each of the first seven abdominal segments, however, there is a group of three or four vertical, striated bands, which lie immediately beneath the body wall and are very tenuous. These may be muscles.

15. The Movements of the Body.

It has already been suggested that the swimming movements of *Culicoides* are peculiar to the family, but it may be that the rapid doubling-up movements of some Chironomid larvae and of *Thaumalea* larvae are related to the *Culicoides* type. I do not know what sort of movement is exhibited by the terrestrial CERATOPOGONIDAE, the FORCIPOMYINAE; but even among the "Vermiformes" the wriggling movement is not universal. *Tetraphora* (= *Dasyhelea*) larvae, for instance, are sluggish and, at best, only bend slowly from side to side. The larva of *Stilobezzia ochracea* moves in a similar fashion, bending the whole body in an arc first to one side and then to the other. This appears to be the basic form of the wriggling movement. The aquatic larva of *Bezzia* moves more quickly and is able to swim. The movement becomes much more rapid in *Ceratopogon* (*Helea*) and *Culicoides*. In some species of *Culicoides*, e.g., *C. impunctatus*, the movement is very rapid, but not very effective, in that the larva makes very slow progress through the water. The

appearance of the larva when it is so moving is that of a vibrating string, with two nodes, one in the region of the metathorax and first abdominal segment and the other in the region of the seventh abdominal segment. In *C. nubeculosus*, a very effective swimmer, the anterior node appears to be shifted forward into the mesothorax-metathorax region, so that the anterior end of the larva is relatively stationary. It is this fact which is probably responsible for the increased efficiency. In *C. albicans*, which is possibly an even better swimmer, there appear to be three nodes, one in the prothorax, one in the region of the first abdominal segment and the third in the region of the seventh abdominal segment. The head, being very near the anterior node, is practically stationary relatively to the body, and this too is probably responsible for the efficiency.

16. *The Oenocytes.*

The oenocytes occur in each of the first eight abdominal segments as small brown objects consisting of clumps of a few cells with large nuclei. They appear with imperfect regularity in the anterior ventral region of the segment. None of them appears to be binucleate.

17. *The Gonads.*

In the mature larva the gonads are present as a pair of ellipsoidal bodies with pointed ends attached anteriorly on each side of the posterior end of the mid-gut and extending backwards into the seventh abdominal segment. The posterior end tapers into a long strand of tissue, which disappears near a clump of adipose tissue apart from the main ribbon of fat body. I have not been able to establish a definite connection between the gonad and this clump of adipose tissue, but Saunders (1924) finds such an association in *Forcipomyia* and, in view of this, one in *C. nubeculosus* is likely.

18. *The Pigment Layer.*

The body pigment, the pattern of which has already been described, occurs in a definite layer, only one cell thick, closely underlying the epidermis. The cells which make up the layer are discoid and their edges overlap. The nucleus of each cell, with a prominent nucleolus, occupies the bulk of the centre of the cell, and round the periphery is a layer of densely packed dark-coloured granules which also extend some way into the cytoplasm (fig. 29). It is easily understood, then, why the pigmentation pattern in the thorax is clearly defined laterally in the mature larva; the layer of pigment cells is shouldered up by the imaginal buds.

19. *The Imaginal Buds.*

Only in the pre-pupal larva are the imaginal buds so large as to affect the shape of the thorax, which then becomes distended. The effect is not so marked as it might be, for at this stage the fat body of the abdomen has also grown, so that the relative proportions are almost unaltered. This is so much so that it is usually possible to distinguish an early pre-pupal larva only by observing the position of the eyes, which, with the beginning of the withdrawal of the head from the old capsule, are retracted towards the posterior margin of

the head. In the late pre-pupal stage the thorax is obviously distended by the evaginated imaginal buds, but here, of course, moulting (but not ecdysis) has already taken place.

The cephalic imaginal buds are a pair of roughly retort-shaped bodies, of which the tubulus of each is directed anteriorly and appears to be involved with the cephalic nerve trunks (fig. 19, *ceph. i. b.*)

The wing-buds appear as discs in the mid-lateral region of the meso- and metathorax. The leg-buds appear as convoluted masses applied to the ventral wall of each thoracic segment.

A well-marked imaginal bud appears applied to the ventral wall of the terminal segment. This, no doubt, gives rise to the genitalia.

The Early Instars.

There are four instars in the larvae of *Culicoides*. This fact is clearly shown by the way in which the head lengths of a collection of larvae fall into four groups. Three measurements of the head were made: total length from the post-occipital ring to the anterior face of the labrum, width at the widest point, and width at the posterior edge of the subgenal ring. The following table shows some average measurements in microns for these dimensions, based on small numbers of *C. nubeculosus*:

<i>Instar.</i>	<i>Length.</i>	<i>Breadth.</i>	<i>Anterior ring.</i>
1st	72	54	40
2nd	122	88	54
3rd	200	122	81
4th	311.5	207	120

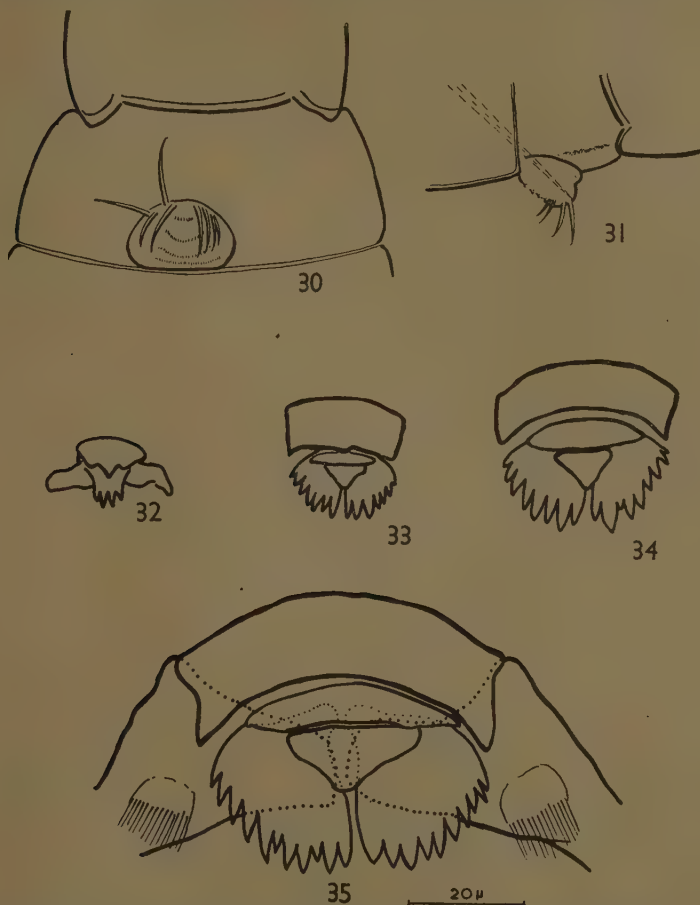
1. The First Instar.

The first instar, on emerging from the egg, swells to about twice the size of the egg. In hatching under the conditions observed, i.e., on damp filter-paper, the larva is greatly helped by the prothoracic pseudopod, with which it hauls itself out. The pseudopod (figs. 30 and 31), like that of the first instar of *C. obsoletus*, which was first observed and pointed out to me by Mr. A. H. Parker, is of a reduced type, approximating closely to that of *Apelma* as described by Saunders (1925), which retains the pseudopod throughout the larval life. It is a simple, fairly large protuberance from the ventral wall of the neck, and posteriorly it abuts on the "intersegment" between the neck and the prothorax proper. The only sign of a possible bilobed or double ancestry is in the fact that the eight long strong setae with which its ventral face is armed are separated to give a small gap in the mid-line, leaving four on each side. Posteriorly the ventral face bears four transverse rows of very small spines. The first instar larva itself is very small of course, and this region in particular is too small to allow the musculature to be worked out with any ease. The only special muscles found are a pair inserted on the mid-line just anterior to the setae and taking their origins somewhere on the lateral wall of the prothorax (fig. 31).

In the newly hatched larva the base of the proleg is invaginated slightly into the neck.

The pharynges (fig. 32) are reduced and the body setae, if present, are too minute to see.

In laboratory cultures the first instar lasts for about three weeks.



FIGS. 30-35.—(30) Ventral view of prothoracic pseudopod of first instar larva. (31) Lateral view of prothoracic pseudopod. (32) The epipharynx of the 1st instar larva in ventral view. (33) The epipharynx of the 2nd instar larva in ventral view. (34) The epipharynx of the 3rd instar larva in ventral view. (35) The epipharynx of the 4th instar larva in ventral view. Figs. 32, 33, 34 and 35 are all to the same scale.

2. The Second and Third Instars.

In the second instar the proleg has disappeared completely. The pharynges (fig. 33) have become a little more complex and more sclerotized. This stage is very short, and in the laboratory lasts for only about one week.

The larva over-winters as the third and fourth instars and emerges the following summer, but nothing is known of the relative length of life in each stage. In the third instar the pharynges (fig. 34) have attained something like the complexity and sclerotization found in the mature larva.

Ecdysis in the Larva.

In larval ecdysis the head is withdrawn from the old capsule and the old cuticle splits along the mid-dorsal line in the prothorax and on to the old capsule, following the course of the epicranial suture as far as the bases of the antennae. The head is thrust out of the split in the prothorax and within

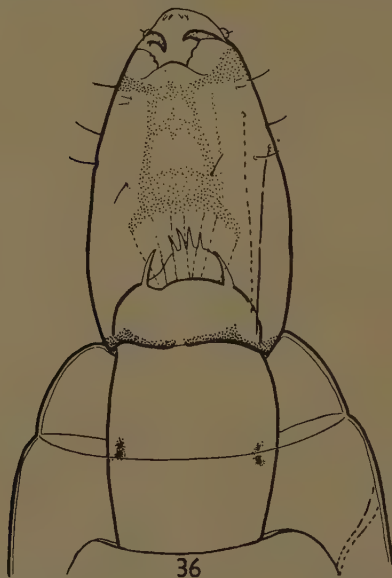


FIG. 36.—An ecdysing larva withdrawing its head from the old capsule. Note the threads attached to two of the sensillae.

two or three seconds the head and the whole thorax emerge from the old cuticle; the lining of the foregut and the salivary duct and its branches as far as their junctions with the glands are rapidly drawn out of the mouth and are caught at the anterior end of one arm of the ecdysial suture. At this stage the old head capsule projects at right angles from the region of the first abdominal segment, the body of the larva still distends the prothoracic segment of the exuviae, the meso- and metathoracic segments of the exuviae are telescoped, and the abdominal segments still fit the larva fairly closely. The next stage occupies a much longer time, and the larva does not so much emerge as drag off the exuviae by catching it in obstructions in worming through the substrate. Occasionally the cast exuviae remains in this condition, but usually it is almost completely telescoped.

In the immediately pre-ecdysis stage, when the head is more or less withdrawn from the old capsule, connecting strands from the head to the capsule, attached to some of the lateral sensillae, are sometimes to be seen (fig. 36). The nature of these strands is unknown; they have not been seen in specimens treated with potash, but this may be because strands of such delicacy are destroyed by the treatment or because they have become involved in other structures. Their presence, however, indicates a hitherto unsuspected deep cuticular strand in the sensillae concerned, analogous perhaps with the axial filament of chordotonal organs.

PUPATION.

Pupation has not been observed in *C. nubeculosus*, but the whole process, leading to a typically successful pupa, has been observed in *C. albicans*, and some of the process, leading to an unsuccessful pupa, has been observed in *C. heliophilus*. It is likely that these processes are largely characteristic of pupation in the genus at least, and an account of the successful pupation is therefore given as indicating what might be expected in the case of *C. nubeculosus*.

The Pupation of C. albicans.

One and three-quarter hours before pupation actually occurred a larva of *C. albicans* was observed to be showing the pupal prothoracic horns evaginated and lying closely pressed against the body-wall within the larval cuticle. Already slightly pigmented, the horns had their bases near the posterior margin of the larval prothorax and curved outwards, forwards and downwards, so that their tips, looked at from the dorsal side, just disappeared beyond the curve of the body in the anterior part of the larval prothorax. The larval eyes were withdrawn towards the posterior border of the head capsule. The Malpighian tubes were conspicuously dark. The position of the prothoracic horn bases, emerging as they do from the anterior end of the pupal prothorax, indicates that the bulk of the larval prothorax at this stage is filled by part of the pupal head.

Ten minutes before pupation the larva began to contract the prothorax longitudinally, the pressure within being thereby obviously increased. These contractions took place at intervals of about two seconds. At the same time active swallowing movements of the pharynx took place, without much movement of the pharynxes, although nothing was clearly seen to be swallowed. It is reasonable to assume that in fact water was being swallowed.

At this stage the caudal spines of the pupa were seen to have become evaginated and to be lying with their tips directed anteriorly, pressed closely against the body-wall by the larval cuticle. It is possible that the caudal spines had been evaginated for some time without having been noticed, for in the pupation of *C. heliophilus* they were observed at a time not less than six hours before pupation. However, in this case pupation was unsuccessful and was possibly very considerably delayed.

The heart rate at this stage was 40 per minute.

Pupation began with the reflection backwards of the caudal spines, so that the larval skin was pushed backwards by their points. The pupa then bulged up into the larval thorax so that the limits of the larval thoracic segments

disappeared in the bulge formed. The larval skin was pushed back more and more by movements of the caudal spines and began to take on the typically wrinkled appearance of the larval exuviae, while the thorax swelled more and more, until the ecdysial suture broke open throughout its length and the anterior part of the pupa burst almost explosively out of the larval skin, trailing the cast lining of the fore gut and the salivary duct attached to the larval head, from the pupal mouth. Within a few seconds the whole of the pupal thorax had emerged, and the fore gut and salivary duct had been completely withdrawn.

The abdomen followed more leisurely, the larval skin being pushed off backwards by the caudal spines and the armed tubercles of the abdominal segments. The whole process, from the initial eruption of the pupal head and thorax to the final discarding of the exuviae, occupied about thirty seconds.

For the next fifteen minutes the pupa, still quite pale except for the prothoracic horns and the caudal spines, lay quietly, with an occasional spasmodic movement. The larval eyes were still evident in the regions of the ventro-lateral tubercles. The abdomen appeared long and slender, being still markedly larval in shape. At the end of this time the fat body of the anterior abdominal region was largely forced up into the thorax in a few spasmodic movements and the thorax took on the characteristic humped pupal shape, while the abdomen became shorter and a little stouter, thus also acquiring pupal shape.

Suddenly, while the pupa lay quiescent, an extensive air space appeared in the region of the proximal part of the left wing bud, and spread in a few seconds, in small definite increments, to the tip of the wing bud and the mid-ventral line. After a pause of a few minutes the air pocket spread across the mid-line into the region of the tip of the right wing bud. Thereafter it spread slowly to the base of the right wing bud.

Half an hour after pupation pigmentation had appeared along the transverse ridge between the bases of the prothoracic horns, along a transverse line immediately posterior to this and as tiny spots at the first abdominal spiracles. Ten minutes later the air pocket had still not reached the base of the right wing bud, the abdominal tubercles and spines had begun to darken and the pupa was still quiescent with occasional squirmings.

Almost an hour after pupation it was again possible to observe the heart, which was then beating at 23 per minute. One hour after pupation the pupa had become completely quiescent and did not respond to probing; ten minutes later the heart beat had become very slow and irregular, so that, although the pupa remained as translucent as ever, it was feared and believed to be moribund. Three and a half hours after pupation the pupa was quite dark. It gave a slight response to probing and the heart was beating at 19 per minute. Six hours after pupation the Malpighian tubes were visible through the darkened cuticle, but the heart was not, and the pupa was transferred to a tube to await the emergence of the adult.

An Unsuccessful Pupation in C. heliophilus.

In this case such of the process as was observed appeared protracted, compared with the successful pupation, and the pupa eventually died before becoming fully pigmented. No air space appeared, and the abdomen did not shorten. This condition is occasionally found in dead or moribund pupae taken from

samples. Experiments by Mr. A. C. J. Weerekoon (private communication) have since indicated that contact with atmospheric air is essential for successful pupation.

THE PUPA.

In the laboratory the pupal stage of *C. nubeculosus* lasts for three to four days.

The pupa (fig. 37) has the form usually found among the Nematoceran

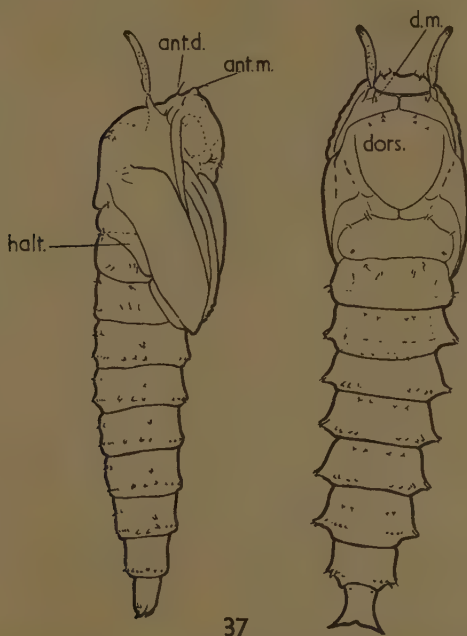


FIG. 37.—Lateral and dorsal views of the pupa. *ant.d.*, antero-dorsal tubercle; *ant.m.*, antero-marginal tubercle; *d.m.*, dorso-median tubercle; *halt.*, haltere.

Diptera. It is about 3.75 mm. long, and has a rather dark brown and well-sclerotized integument which is particularly dark and nodular in the region of the mesothoracic hump. This hump is formed by the strong inclination of the prothorax and the head to the long axis. The cephalothorax as a whole is compact and rigid, but the abdomen, which is usually carried in the longitudinal axis of the meso- and metathorax, is mobile and may be found curved in any direction. Both cephalothorax and abdomen bear armed and seta-bearing tubercles which have been named and figured by Carter, Ingram and Macfie (1921), in their account of *C. accraensis* and other *Culicoides* species, because of the specific value of the size and arrangement of these tubercles.



FIGS. 38, 39.—(38) Lateral view of the head of the pupa. *ant.d.*, antero-dorsal tubercle; *ant.m.*, antero-marginal tubercle; *d.l.*, dorso-lateral tubercle; *omm.*, pupal ommatidia; *v.l.*, ventro-lateral tubercle; *v.m.*, ventro-medial tubercle. (39) Operculum, carrying antero-marginal tubercles.

1. The Head (fig. 38).

The head is clearly marked off from the rest of the cephalothorax, especially in a lateral view. The base of the antenna arises in the lateral region near the anterior end and the antenna itself curves back over the eye to reach and run between the anterior border of the wing and the tibia of the mesothoracic leg for a short distance. In the region of the eye, i.e., immediately posterior to the base of the antenna and extending a little dorsad and ventrad, there are a number of small domed protuberances, more or less regularly arranged in a diffuse honeycomb pattern (fig. 42, *p. eye.*). In the maturing adult within, where the eyes are visible, they are withdrawn from the integument and bear no relation to these protuberances except the resemblance of pattern, but there is little doubt that the first ommatidia, at any rate, are laid down on these "formers" in the integument.

The dorsum of the head is occupied largely by the "operculum" (fig. 39), which is bounded by the arms of the ecdysial suture and therefore corresponds to the fronto-clypeus. The arms of the suture do not converge anteriorly, so that when the adult emerges, the operculum, a convenient name to retain, is simply reflected forward, as on a hinge, and returns more or less to its original position after the adult has emerged. The anterior border of the operculum bears two large tubercles, which each carry a single, large, articulated seta. These are the *antero-marginal* tubercles (figs. 37, 38 and 40). The rest of the operculum is beset with small, dark spinules slightly inclined forwards. They are particularly large anteriorly and tend to become fewer and smaller posteriorly.

Slightly laterad of the operculum and posterior to the anterior marginal tubercle is another large tubercle, the *antero-dorsal* (figs. 37, 38 and 40), which bears one large articulated seta and a small articulated seta mesad of the first.

In the posterior ventral region of each side of the head, near the mid-line, there is a single small seta without a tubercle, the *ventro-median* (figs. 38 and 42, *v. n.*). Dorsad of this there is a roughly triangular postero-ventral projection of the head, posterior and ventral to the pupal eye, which is markedly nodular along its posterior border, some of the nodules grouping themselves to form the sides of a conical protuberance which is not otherwise armed. The ventral border of the projection bears two short thin setae on a very small rounded tubercle, the *ventro-lateral* (figs. 38, 40 and 42, *v. l.*).

2. The Thorax.

The respiratory trumpets, which are situated on the prothorax, will be described and discussed later.

Laterad of the prothoracic horns and just dorsad of the antennae there is on each side a projection of the lateral wall of the prothorax bearing a tubercle, the *dorso-lateral* (figs. 38 and 40), from which arise two setae, one dorsal and slightly posterior, the shorter, and one ventral and anterior, about twice as long as the first. A border of fine nodules extends from just ventrad of the prothoracic horn bases, curving round posterior to the dorso-lateral tubercles and passing just dorsad of the antennae, and almost reaches the cleft which marks the anterior edge of the wing.

On the dorsal hump of the thorax are a number of tubercles and setae, the *dorsals* (figs. 37 and 40).

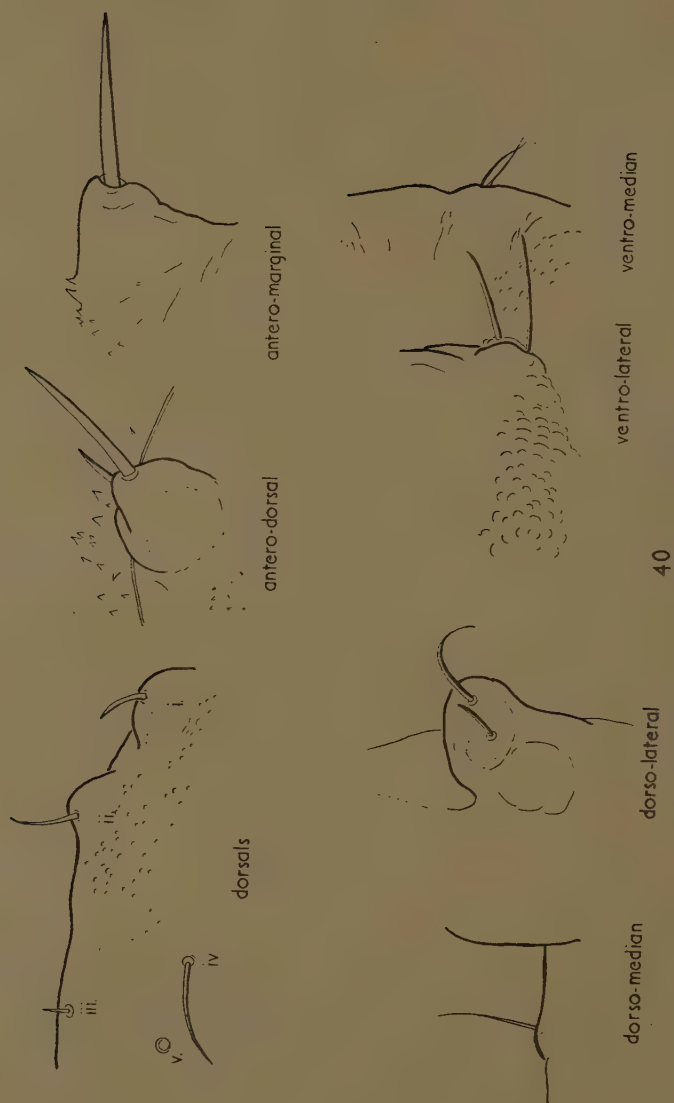


FIG. 40.—The tubercles of the head and thorax of the pupa.

These consist of :

- i. a small well-sclerotized tubercle bearing a short, slender, articulated spine ;
- ii. a structure similar in shape and size to (i), slightly posterior and mesad ;
- iii. a small spine or thick, articulated seta, without tubercle, posterior to and slightly mesad of (ii) ;
- iv. a seta, about as long as the spines of (i) and (ii), without a tubercle, posterior to and well laterad of (ii) ;
- v. a sensilla, looking very like (iv) without its seta, posterior to (iv) ;
- vi. a single sensilla, well apart from the others, on the posterior margin of the wing, very near its root.

In addition, there is a single fine seta just mesad of each prothoracic horn ; this has not been mentioned elsewhere. It may be called the *dorso-median* (figs. 37 and 40).

The prothorax is marked off from the mesothorax by a transverse furrow immediately anterior to the hump. The mesothorax is well indicated by the presence of the large wing buds. Dorsally, its posterior margin, the scutellum, is prolonged backwards in a broad curve and indents the anterior margin of the metathorax. In other species there is sometimes a further peg-like prolongation in the mid-line which may actually project beyond the posterior margin of the metathorax, but this feature is not always constant. In *C. nubeculosus* the metathorax is completely divided in the mid-dorsal line, although the sclerotized margins of the divisions are usually closely applied to each other ; but in some exuviae there is an obvious separation (figs. 37 and 41).

Laterally the metathorax bears the buds of the halteres. These are very like the wing buds in appearance, but that the distal part is attenuated, and the basal part relatively enlarged. Their origin is thereby clearly indicated (fig. 37, *halt.*).

The metathorax also bears a single seta, the *postero-dorsal*, near the anterior margin in the dorso-lateral region.

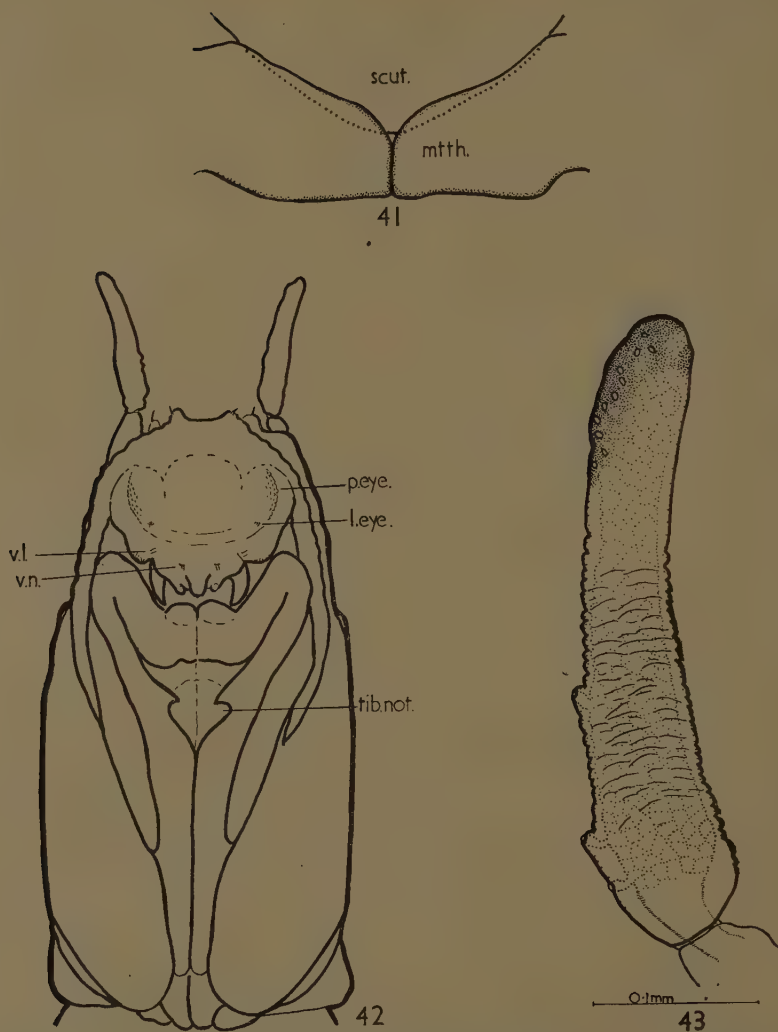
On the ventral side there is a curious notch and hook on the mesal side of the tibia of the prothoracic leg. This is present not only in the species of *Culicoides* examined, but also in some closely related genera, and according to Saunders' figure of *Forcipomyia* it is present there also. It is likely then that it appears throughout the family (fig. 42, *tib. not.*).

The metathoracic spiracle is not evident.

3. The Abdomen.

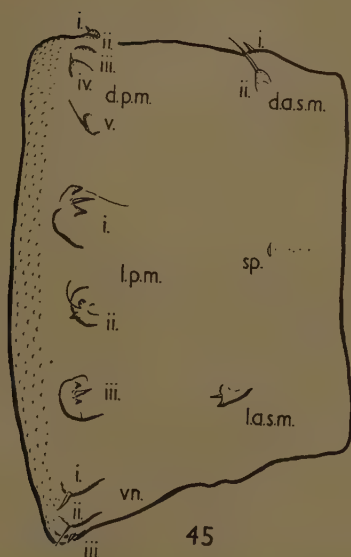
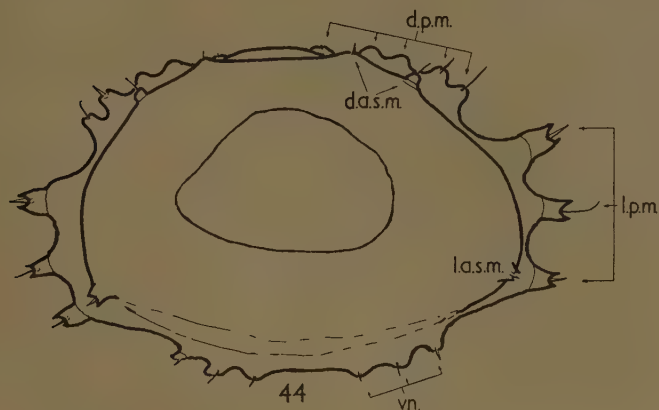
The abdomen is mobile, and seems to be used by the pupa for manoeuvring itself into a favourable position. The first segment is partly overlapped and obscured by the halteres, wings and legs. The spiracle of this segment is large and clear, particularly in the exuviae, although it is covered by the haltere. Its situation very near to the anterior border makes it appear at first sight to belong to the metathorax, especially as no other spiracle of the metathorax is to be seen, but there is no doubt that this spiracle belongs to the first abdominal segment.

The tubercles of the first and second abdominal segments are reduced and represented only by setae, and their homologies will best be recognized by



FIGS. 41-43.—(41) Dorsal view of the mid-dorsal region of the thorax. *mtth.*, metathorax; *scut.*, scutellum. (42) Ventral view of the head and thorax of the pupa. *l. eye.*, larval eye; *p. eye.*, pupal eye; *tib. not.*, tibial notch; *v.l.*, ventro-lateral tubercle; *v.n.*, ventro-median tubercle. (43) Lateral view of the prothoracic horn.

reference to those of the fourth abdominal segment, which may be taken as representative (figs. 44 and 45).



FIGS. 44, 45.—(44) Anterior view of isolated 4th abdominal segment of the pupa. (45) Lateral view of the 4th abdominal segment of the pupa. *d.a.s.m.*, dorsal antero-submarginal tubercles; *d.p.m.*, dorsal postero-marginal tubercles; *l.a.s.m.*, lateral antero-submarginal tubercles; *l.p.m.*, lateral postero-marginal tubercles; *sp.*, spiracle; *vn.*, ventral tubercles.

There are five groups of tubercles in the fourth abdominal segment, comprised of the following :

- A. In the dorso-lateral region near the anterior margin, the *dorsal antero-submarginals*, consisting of—
 - i. a dorsal tubercle with a short stout seta,
 - ii. a lateral tubercle with a fine seta about one and a half times as long as (i).
- B. In the dorso-lateral region near the posterior margin, the *dorsal postero-marginals*, consisting of—
 - i. a small sclerotized tubercle near the mid-dorsal line, with a very small seta,
 - ii. a very small tubercle with no seta,
 - iii. as (ii), but larger tubercle,
 - iv. a large tubercle with a short stout seta,
 - v. a large tubercle with a long thin seta.
- C. In the lateral region near the posterior margin, the *lateral postero-marginals*, consisting of—
 - i. a large tubercle dorsally, with two spines and a short stout seta, about the size of one of the spines, set in the fork ;
 - ii. a tubercle similar to (i), but with a very thin seta in the fork, about $1\frac{1}{2}$ times the length of a spine ;
 - iii. a tubercle similar to (i), ventrally, and also with a short stout seta in the fork.
- D. About level with (iii) of c, midway along the segment, a single tubercle, like that of (iii), but with shorter spines and a longer stout seta in the fork, the lateral *antero-submarginal*.
- E. In the ventro-lateral region near the posterior margin, the *ventrals*, consisting of—
 - i. a large simple tubercle laterally, with a short stout seta,
 - ii. a similar tubercle with a thin seta about twice as long as that of (i),
 - iii. another similar tubercle ventrally, with a short stout seta like that of (i).

The spiracle is present as a thin, crescentic sclerotization in the mid-lateral line near the anterior margin of the segment.

The posterior margin of the segment has a broad border of closely packed small nodules. This is a feature of all the abdominal segments except the last.

The anterior margin has a border of spinules, not so closely packed as the nodules of the posterior border. This is a feature of all the segments except the first.

The tubercles of the third to the seventh segments are almost identical with those of the fourth in position and character, but that the spines of the lateral postero-marginals become rather larger and the two ventralmost tubercles of the dorsal postero-marginals develop small lightly sclerotized spines.

There are no tubercles as such in the first abdominal segment : they are represented only by setae (fig. 37). In the area bounded anteriorly by the posterior border of the haltere mesad of its anal lobe there is a slight swelling

which bears a group of three setae, the most anterior being short and rather stout and the other two long and slender. Laterally, again near the posterior border of the haltere, behind its anal lobe, there is another group of three setae of approximately equal size. Dorso-laterally, near the posterior border, are a sensilla, a short fine seta and a longer fine seta. Ventrally there are no setae to be seen. Like the other segments the first has a posterior border of closely packed small nodules.

In the second segment there are representatives of almost all the typical tubercles. The first dorsal antero-submarginal is small; the second is represented by a long thin seta on a lightly sclerotized patch which can hardly be called a tubercle. The dorsal postero-marginals are typical, but much reduced and only lightly sclerotized. The lateral postero-marginals are only setae on slightly raised areas, the first and third setae being short and the second about twice as long as the others. There is no lateral antero-submarginal. The ventrals are visible through the exuviae, from the dorsal side, as three small setae.

In the eighth segment (fig. 37) all the tubercles are large, but they are set round the posterior margin and there are only seven on each side. They consist of—

- a. A spined tubercle with a short stout seta.
- b. A spined tubercle with a long seta.
- c. A double-spined tubercle with a stout seta in the fork.
- d. A spined tubercle with a long thin seta.
- e. A double-spined tubercle with a stout seta in the fork.
- f. A simple bulbous tubercle with a single thin seta.
- g. A simple tubercle with a stout seta.

The dorsal postero-marginals are probably represented by a. and b., the lateral postero-marginals by c., d. and e., and the ventrals by f. and g.

The last abdominal segment is without tubercles and terminates in a pair of laterally curving sharp-tipped processes, the points of which are sclerotized and darkly pigmented and directed at an angle of about 60° to the long axis (fig. 37). The base of each of these large spines is partly covered with small scaly spines and the lateral face bears a pair of sensillae. As in the other segments, there is an anterior border of spinules.

I found no pigmentation pattern on the abdomen such as is found in some other species, and has been described and figured in *C. nubeculosus* by Mayer (1934).

4. The Respiratory Trumpets (fig. 43).

The respiratory trumpet or prothoracic horn of each side arises from a large tubercle at the lateral border of the prothorax. The tubercle is followed by a short "segment," beyond which is the main part of the trumpet, a rather long, flat-sided, ventrally curving process which projects beyond the head. The spiracular chamber arises from the prothorax of the adult, well posterior to the base of the trumpet, and runs forward beyond the short segment into the felt chamber which occupies the main part of the horn. The difference between the spirally strengthened wall of the spiracular chamber and the cellular wall of the felt chamber is quite clear. There is no trace of the closing

mechanism described in *Psychoda* pupae by Satchell (1948). There is an incomplete ring of sclerotization at the origin of the spiracular chamber, but this may be the rudiment of the prothoracic spiracle of the adult.

On the pupal wall, externally to the spiracular chamber, and running in the same line, there is a thin line of sclerotization which is probably the "scar of the tracheal extension" of Satchell.

The main part of the prothoracic horn is pale except for the tip, where there is a deeply pigmented area extending from some way behind the tip on the dorsal side to a point not quite so far back on the ventral side and also spreading a little along the sides. The surface of the basal two-thirds of the horn is marked by irregular, wavy lines which are the anterior edges of plate-like outgrowths closely applied to the wall and over-lapping each other. In most other species these are represented by an imbricated series of scales.

Tubular extensions from the felt chamber reach the surface of the horn, where they appear as very thin-walled, low, domed projections. They are present at the tip, closely packed in an irregular line extending the length of the pigmented area. A few are also present in the proximal half of the horn and here they are raised on tubercles. Their numbers are not constant, not even in the two horns of the same individual. On the basis of twelve specimens examined, there was a range of 14 to 17 round the tip, and a range of 1 to 4 in the basal two-thirds, with a preponderance of 3.

Some importance for purposes of identification has been attached to the number of spiracular papillae, and where species are not closely related the difference in numbers is probably greater than the range; but among closely related species the ranges may overlap so that the number of papillae becomes an unreliable character. The same remarks apply to the operculum, which has also been used for identification purposes. The character of the anterior marginal tubercles, which are present on its anterior margin, appears to be constant, but the distribution and density of the spinules on the surface of the operculum vary from individual to individual.

In specimens from Dorset the degree and extent of the pigmentation of the prothoracic horn were constant. The pigment was a transparent black, through which, in mounted specimens, the felt chamber and the papillae could be distinctly seen; it occupied only the distal quarter to one-third of the horn, which elsewhere was quite unpigmented. In Scottish forms from Inverness-shire the pigment appeared to extend slightly further down the horn and, near the tip, was so dense that, even with a strong light, it was not possible to see the felt chamber and all the distal papillae. In another Scottish form, taken in Ayrshire by Mr. F. W. Edwards in 1921 [British Museum (Natural History) Collections], there was a distinct basal ring of transparent black pigment in addition to the distal pigment. It thus appears probable that the species is not homogeneous.

5. *The Relation between the Larval and Pupal Setae.*

It is possible to suggest a relationship between the abdominal setae of the larva and of the pupa.

"1" and "2" of the larval abdomen clearly correspond to "i" and "ii" of the dorsal antero-submarginal of the pupa. "3" corresponds to the lateral antero-submarginal; "10," "11" and "12" to the ventrals; "4,"

"5" and "6" to the lateral postero-marginals; and "8" and "9" to "iv" and "v" of the dorsal postero-marginals; seta "i" of the dorsal postero-marginals is very tiny, while "ii" and "iii" are merely tubercles. The pair of setae "7" of the larval abdominal segments have no homologues in the pupa.

The relationship in the head and thorax is less clear, and it can only be guessed that the antero-marginal of the pupa corresponds to "t," or possibly "q" of the larva; the antero-dorsal to "p"; the ventro-median to the paired setae "x" and the ventro-laterals to the paired setae "o."

THE MORPHOLOGY OF THE HEAD.

The fusions and overgrowths of the cranial sclerites which have taken place in the larva of *Culicoides* have produced a condition in which only one sclerite—that embraced by the arms of the ecdysial suture—can be identified by direct means. The problem of the origin of the rest of the capsule finds a possible solution only in reference to the larval heads of more primitive Nematocera.

I have said that one sclerite can be identified by direct means, but, in fact, there is some confusion about the names which should be applied to the sclerite and to its bounding suture. This confusion is due to a controversy as to the real nature of sclerites and sutures. Some general considerations of the position, while not especially illumined by the case of *Culicoides*, may yet have some value.

1. General.

The simple fact that it is possible to a greater or lesser extent to homologize the principal sutures of the insect head from group to group among the major orders at least is an indication of some deep-rooted significance attached either to the sutures themselves or to the sclerites they circumscribe or to both. What the precise nature of this significance may be, and notably, whether it has anything to do with segmentation, is a matter of controversy. Since the days of Savigny (1816) the theories of the segmentation of the head have been based on a consideration of the head appendages, either in the adult and larva or in the embryo. Not until Comstock and Kochi (1902) was there any real attempt to ascribe segmental significance to the head sclerites themselves. Their reconstruction gained little support. The generally held view is that sclerotization is secondary and, with the possible exception of the post-occiput, has no metameric significance.

In the past few years, in a series of papers, Ferris and his co-workers have made a praiseworthy attempt to re-establish morphology on a more satisfying basis by interpreting the head sclerites in terms of a segmental theory.

Both DuPorte (1946) and Snodgrass (1947) have pointed out that the sutures themselves are of at least four different kinds: lines of rupture; lines of thickening of cuticle; lines of inflection of cuticle; and lines of possible real union between adjacent sclerites. Neither indicates what physical characters a line of real union might be expected to show, beyond referring to the post-occipital suture as such a possible line. The fact that the first three types are functional is, of course, no reason why they should not also have morphological significance, but they may well have been secondarily

developed. DuPorte has drawn a clear picture of the way in which inflected sutures might have evolved to fill functional needs.

2. *The Ecdysial Suture and the Clypeus.*

DuPorte and Snodgrass have also pointed out that one suture in particular, the epicranial suture, is markedly different from the others in being, not a line of strengthening, but a line of weakening; in fact that it is the line along which rupture takes place at ecdysis. They have therefore called it the ecdysial line. This is obviously a functional suture, while at the same time there is some evidence that it has considerable morphological significance.

At an early stage of the insect embryo, when the appendages have begun to form, the head is represented by an anterior median lobe and a lateral lobe on each side of, and slightly posterior to it. When dorsal closure takes place the median and lateral lobes are reflected dorsally and fuse when they meet, along a Y-shaped line. Comstock and Kochi derive the frons, clypeus and labrum from the median lobe, and this derivation, apart from the frons, is also made by Johannsen and Butt (1941). It was suggested by Comstock and Kochi that the epicranial suture marks the line of fusion of the cephalic lobes with each other and with the median procephalic lobe.

This is an attractive suggestion and, if true, would appear to give major significance to the epicranial suture; on the other hand, the variability of this suture presents us with the alternatives of believing that the suture throughout its length is significant, and that other features, such as the position of the antennae relative to the cephalic lobes, are variable, or that these features are constant, while the anterior ends of the arms of the suture are not significant, in which case the significance of the whole may be whittled away almost without limit. Furthermore, as Snodgrass points out, if the epicranial suture were of such fundamental importance, it should also occur among other arthropods, but, other arthropods have different ways of ecdysis. Other classes of arthropods, however, may have different methods of dorsal closure, so that then this criticism would not apply. Moreover, it may exist as a morphological entity without being developed for the function it serves in insects. However this may be, it is clear that the epicranial suture merits further consideration.

The whole problem is made more difficult by the variation of the internal anatomy of the head, so that in referring sclerotization to internal anatomy or vice versa one is apt to find oneself sometimes arguing in a smaller circle than usual. It is nevertheless regrettable that DuPorte, in studying the variation of the sutures in the main orders, should have dismissed the possibility of deriving any information from the muscle origins. A simultaneous investigation of their variation would have left him in a position to indicate how far the variation was independent of that of the sclerites. Snodgrass, however, points out that there are limits to the variation of the internal anatomy so far as the relation of the origins of some of the muscles to the epicranial suture is concerned, and that the shift of muscle origins is infrequent enough for them to be used as a general criterion for the determination of some of the individual sclerites. He writes that the arms of the ecdysial suture "always run through the cranial areas that intervene between the attachments of the mandibular muscles and those of the facial muscles" (*loc. cit.*, p. 45).

Hinton (1947) opposes a number of the views expressed by Snodgrass (1947). The main points of his criticism are directed against Snodgrass' assertion of the relation between the course of the epicranial suture and the attachments of the mandibular and facial muscles. On a subsidiary point he produces evidence that, in some caterpillars, as illustrated by *Polia nebulosa*, one pair of the dorsal pharyngeal muscles has its origins laterad of the arms of the epicranial suture, thus conflicting with Snodgrass' (1947:34) dictum that ". . . precerebral dilators of the pharyngeal region of the stomodaeum . . . in all insects are consistently frontal muscles." This dictum, however, is a lapse on Snodgrass' part, for in his *Principles* (1935:286) he points out that one or more pairs of the "dilatores pharyngis postfrontales" arise on the post-frontal region, and are inserted on the pharynx within the loop formed by the frontal ganglion connectives and anterior to the brain. From Hinton's figures it is difficult to be certain whether the pharyngeal muscles he refers to belong to an anterior group or to the "dilatores pharyngis postfrontales," in which latter case, of course, their origin laterad of the epicranial suture would not be abnormal.

More important, Hinton finds also that in some caterpillars, some of the mandibular adductors originate on the sides of the deep internal ridge, which is an inflection of the area between the arms of the epicranial suture, and, thus, that the mandibular and facial muscle origins are not, in fact, always separated by the arms of the epicranial suture. Hinton himself remarks that the head of the caterpillar "is unusual in possessing a relatively enormous occipital foramen and a strong dorsal Y-shaped internal ridge," and that the origin of this ridge is "probably connected with the structural weakness of a head with so large an occipital foramen." There seems no doubt that in this lies also the explanation of the exception to the rule formulated by Snodgrass. This, at least, is clear, that Snodgrass' rule is widely applicable but, in cases of unusual modification, where it would be most valuable, is not to be relied upon. It is difficult to see how the rule could be applied in, for instance, the Vespid figured by Snodgrass (1947), where the coronal stem extends to the labrum and thus has no anterior arms.

Reference to Snodgrass' figure of the orthopteroid head shows that he makes use of another feature in determining the relations of the head structures. This feature is the position of the frontal ganglion and its connectives. The frontal ganglion lies just above and behind the morphological mouth, and its connectives loop over the retractor muscle of the mouth angle and enclose the insertions of the pharyngeal muscles, thus separating them from the muscles of the labrum and cibarium. There can be no doubt that this feature is significant. One cannot but be impressed by the fact that in larvae such as that of *C. nubeculosus*, where the brain has been retracted into the prothorax, the frontal ganglion remains within the head, just behind what is to be regarded as the morphological mouth.

Unfortunately, the position of the frontal ganglion has no special relation to the epicranial suture, for the groups into which the head muscles are divided are not the same in each case. The only relation the position of the frontal ganglion has to the capsule is that it separates the muscles which have their origin on the clypeus, the dilators of the cibarium and of the mouth, from those which have their origin on the frons, the retractor of the mouth angle and the

anterior pharyngeal muscles. This is of doubtful value, for the frons is coming to be regarded rather as a vague anatomical region than as a definite morphological entity. In any case, it appears to be uncertain that the clypeus is always marked by having the cibarial muscles inserted upon it, for Dorsey (1943) has found an apparent exception in the Curculionid beetle *Pantomorus leucoloma*, where, according to his figure, the cibarial and pharyngeal muscles take their origin on what he calls the "frons." Ferris (1944) regards this anomaly as a misinterpretation and maintains that Dorsey's "frons" is in fact clypeus.

In *C. nubeculosus* the position is clear cut. The anterior part of the sclerite bounded by the arms of the epicranial suture, having upon it the origins of the dilator muscles of the cibarium and the mouth, this latter being probably represented by the levator of the epipharynx (figs. 19 and 21, *epi. lev.*), is undoubtedly the clypeus. The posterior part, bearing the origins of the retractor of the mouth angle and the anterior pharyngeal muscles, corresponds to the frons.

3. Lines of Real Union.

Snodgrass (1947) remarks that the term "suture" can be applied only to lines of union between separate centres of dermal hardening. Unfortunately, one does not find centres of sclerotization in the sense that one finds centres of ossification. Ferris (1943), attempting to interpret the head sclerites in terms of a segmental theory, appeals to the analogy between sclerotization and ossification. This appears to be ill-conceived, for the segmentation of the vertebrate skull has been worked out on embryonic ossification centres, and if any analogy is to be drawn, it should start from the fact that the vertebrate morphologists found themselves in great difficulties on attempting to derive the origin of the head from a consideration of the post-embryonic structures.

Hinton (1947), in a footnote (p. 843), "sees no objection to retaining the term suture in the loose sense in which it has been used for more than a century by entomologists." There can be no objection now, of course, to its use in a loose sense, so long as it is clearly understood that it is being used only in a loose sense, for otherwise it is liable to be interpreted in the precise sense which gives to the lines so described morphological significance they may not have. Ferris, I believe, has been thus misled into giving greater significance to sutures than he is able to demonstrate they hold.

The post-occipital suture is generally regarded as a real or intersegmental suture; but it has, in itself, no characters, apart from the presence on its course of the posterior tentorial pit, which clearly mark it off from other sutures of the same inflected type. This may mean either that all similarly inflected sutures are also intersegmental, which is improbable, or, much more probably, that nothing is to be gained from an attempt to differentiate between "real" and "secondary" sutures on the basis of their superficial nature.

4. The Lateral and Ventral Walls of the Cranium.

No deductions about the sclerites which have gone to form the undifferentiated lateral and ventral walls of the cranium of *C. nubeculosus* can be made

from a study of *C. nubeculosus* itself, but some attempt at a solution may be made from a study of other families of Nematocera. Fortunately the material exists in a paper by Anthon (1943a) and one by Cook (1944a). Anthon deals with the head structures of the TRICHOCERIDAE, PHRYNEIDAE (= ANISOPODIDAE, = RHYPHIDAE), LIRIOPEIDAE (= PTYCHOPTERIDAE) and PSYCHODIDAE. The PHRYNEIDAE, TRICHOCERIDAE and PSYCHODIDAE present a series in which the ventral wall of the cranium is initially membranous and subsequently becomes increasingly sclerotized, apparently by extensions of the lateral walls, so that in *Philosepedon* (PSYCHODIDAE) the resemblance of the ventral wall to that of *Culicoides*, particularly those species which show a median posterior suture on the ventral wall, is very considerable. A further development from the series takes place in LIRIOPEIDAE, where the ventral wall becomes secondarily differentiated. The series is well shown in Anthon's figures.

Anthon himself points out that this series is linked via *Philosepedon* to the CULICIDAE, particularly to *Culex* itself, and suggests that a closer linkage may be found through *Bittacomorpha* (LIRIOPEIDAE). Malloch's (1915) figure of the larval head of *Bittacomorpha* suggests such a relationship, but it is too simplified for much to be derived from it.

Cook deals with the larval heads of the CULICIDAE, and his figures of *Anopheles maculipennis* and *Armigeres malayi* bear an obvious resemblance to those of *Philosepedon*. The relation of the sutures labelled "premaxillary" by Cook to the structures described by Anthon will be discussed later.

There seems to be little doubt that Anthon's interpretation of the development of the anterior part of the ventral wall is correct. He suggests that the thickened ridges below the sub-genal suture in *Mycetobia* (PHRYNEIDAE) have extended ventrally until, in *Philosepedon*, they fused in the mid-line and then extended forwards to form a "hypostomium" which covers the labium. *Thaumalea* (THAUMALEDIDAE), which he does not deal with, appears to fit into this series between TRICHOCERIDAE and *Philosepedon*.

The posterior part of the ventral wall, he suggests, has been similarly developed by the ventral extension of the post-genae, which have fused in the mid-line to form a "hypostomal bridge," part of the line of fusion being marked, as in *Philosepedon*, by a short, median, posterior suture. This suture is also present in some CULICIDAE and some species of *Culicoides*, notably in *C. delta* and *C. halophilus*, and also in *Stilobezzia ochracea* and *Ceratopogon* sp. This interpretation, however, is questionable, even for the groups dealt with by Anthon himself. It requires that the posterior part of each sub-genal suture, the hypostomal suture, ending in the posterior tentorial pit, should be displaced towards the mid-line to meet and fuse with its fellow of the other side. This condition is well illustrated in Snodgrass' figure of an adult *Vespa* (*Principles* : 122, fig. 65b). But, even on his own figures, this does not appear possible, for the sutures to be seen on the ventral side of the head of *Trichocera* in his figures he elsewhere refers to as the "hypostomal" sutures. If they were indeed the hypostomal sutures, then the sclerotized area lying between them could not possibly be derived from the post-genae, for the hypostomal sutures form the ventral boundaries of the post-genae. On closer inspection, however, it is seen that their anterior ends are not connected to the anterior parts of the true sub-genal sutures which lie along the dorsal edges of the sub-genal ridges; moreover, their posterior ends do not connect with the posterior

tentorial pits. These sutures cannot therefore be the true hypostomal sutures, and are presumably secondarily developed, in which case they can give us no reliable information.

Cook (*loc. cit.*), in discussing the CULICIDAE, puts forward a more satisfactory interpretation for the development of the ventral wall. He suggests that it is formed by the forward extension of the ventral parts of the post-occiput. There is nothing in *Trichocera* or the CERATOPOGONIDAE which precludes this interpretation, and it is supported by Cook's figures of *Theobaldia incidens* and *Armigeres malayi*, where there is shown a complete and well-developed hypostomal suture (its anterior end connecting with the sub-genal suture and its posterior end passing through the posterior tentorial pit), the existence of which precludes any ventral extension of the post-genae, while it readily permits the forward extension of the post-occiput. It should be noted that Cook, writing in terms of a segmental theory of sclerotization, describes the post-occiput as the maxillary segment and the hypostomal sutures as the pre-maxillary sutures.

It will be assumed, then, that Cook's interpretation is valid for the CERATOPOGONIDAE also, so that the lateral walls of the head capsule in *Culicoides* are to be regarded as the post-genae, while the ventral wall is formed from the forward extensions of the post-occiput, the hypostomal suture marking the division between the post-genae and the post-occiput having been lost, and the suture marking the line of fusion of the two lobes of the post-occiput being present as a short median suture only in some species.

5. The Anterior Sclerotizations of the Head.

As in the case of the lateral and ventral walls of the cranium, it is possible to learn something of the origin of the sclerotized structures surrounding the functional mouth in *C. nubeculosus* from a consideration of the structures found in the groups studied by Anthon and by Cook. The structures found in *Mycetobia* and *Phryne* (= *Rhyphus*) (PHRYNEIDAE) (fig. 46) are particularly illuminating. The thickened "sub-genal ridge" (*sg. b.*) clearly corresponds to that found in *C. nubeculosus*, the main difference between them being that in *Phryne* the ridge of each side does not meet and fuse with its fellow in the mid ventral line. This fusion takes place in *Philosepedon*. Another difference is, that there is an evident anterior tentorial pit in *Phryne* whereas in *C. nubeculosus* it is not apparent.

In *Philosepedon* the fused sub-genal ridges give off an anterior extension in the mid-line, covering the labium, which is withdrawn into the functional mouth. Anthon shows this in section. Despite the reduction of the labium to a rudiment and the further extension of the hypostomium in *C. nubeculosus* (fig. 10), the resemblance is sufficiently great to make it clear that the same process has taken place there.

Anthon's interpretation of the structures at the upper end of the sub-genal ridge is not altogether satisfactory. The anterior arm of the tentorium is obviously correctly named by him, but why he should regard the extension from it to the cranial wall *below* the antenna as the dorsal arm of the tentorium and ignore the extension *mesad* of the antenna is not clear. Nevertheless, he is right in doing so, for in the CULICIDAE, Cook finds a structure invaginated from the cranial wall *mesad* of the antenna. Cook rightly names this a

phragma—the “paraclypeal phragma”—and it therefore cannot be the dorsal arm of the tentorium. In the CULICIDAE also Cook finds what is left of the dorsal arm of the tentorium—the “post-antennal buttress.”

The anterior extension of the paraclypeal phragma in *Phryne* Anthon regards as the “epistomal ridge” because it originates laterally in the anterior tentorial pit, although it is short, directed anteriorly, and does not fuse with its fellow of the other side. He goes on to suggest that the small sclerite attached to the anterior end of each of these projections is one half of the clypeus which, as a whole, has been thrust apart by the division and swivelling forwards of the “epistomal ridge” on its lateral ends. Consequently, he regards the whole area between the arms of the ecdysial suture and the labrum as the frons. This seems hardly likely and it cannot be assessed from other evidence, for he gives no account of the muscle attachments. This situation, however, appears not to arise in *Culicoides*.

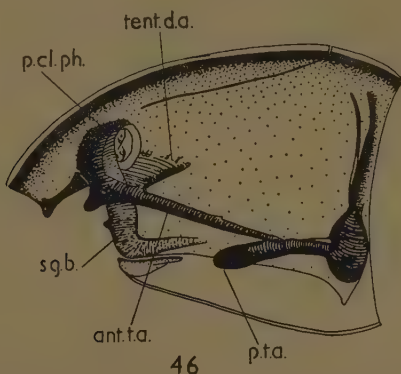


FIG. 46.—Right half of head capsule and tentorium of the larva of *Phryne* (after Anthon). *ant.ta.*, anterior arm of the tentorium; *p.cl.ph.*, paraclypeal phragma; *p.ta.*, posterior arm of the tentorium; *sg.b.*, subgenal band; *tent.da.*, dorsal arm of the tentorium.

The tentorial structures present a series beginning with PHRYNEIDAE, where there is a complete and well developed tentorium, through TRICHO-CERIDAE, where the posterior arms are much shortened, and LIRIOPEIDAE and some of the CULICIDAE, where the anterior arms unite as very thin strands with the posterior pits, ending in PSYCHODIDAE, where they are completely absent. They are also absent in *Chironomus* (Cook, 1944a). In this series *C. nubeculosus* appears to fit somewhere between the LIRIOPEIDAE and CULICIDAE on the one hand and the PSYCHODIDAE on the other.

It should be noted that in *Mycetobia* and *Phryne* in the region in which the paraclypeal phragma and the arms of the tentorium meet there is a process on which the mandible has its inner articulation. A similar process is present in *C. nubeculosus*, but in the CULICIDAE it is greatly lengthened and fuses ventrally with the labial structures; nevertheless, it still bears the inner articulation of the mandible. Cook names it the cibarial bar.

In *Forcipomyia*, as described by Saunders (1924), where the antennae are set well back on the head, the anterior head skeleton is less complex than it is in *Culicoides*, because of the absence of the "sub-antennal rings"—the complex made up of the dorsal arm and paraclypeal phragma. A similar state probably occurs in *Thaumalea*. In both these genera the head is hypognathous, so the displaced position of the antennae results in their being directed anteriorly, and in a shift of some of the articulations from their positions in the prognathous type. The inner articulation of the mandible is obscure in Saunders' figure of *Forcipomyia*; it appears to be on the "pre-mandibles." The "pre-mandibles" themselves articulate with an inward extension of the dorsal wall of the capsule. In *Apelma* (CERATOPOGONIDAE), where the antennae are set immediately above the bases of the mandibles, it will very likely be found that there are "sub-antennal rings." The differing habits are to be correlated not only with the posture of the head, but also with its sclerotizations.

In *C. nubeculosus* the anterior arm of the tentorium has a curious relation to the cibarium, running along the dorsal edge of its lateral extension and actually appearing to support it. Neither Anthon nor Cook give an account of the soft parts which enables it to be seen whether a similar situation exists in the groups they describe. Saunders does not clearly show the relations of the apparently corresponding rod in *Forcipomyia*, and remarks that anteriorly it is "embedded in the side of the labrum." Since there is no sclerotized antennal complex in *Forcipomyia*, the nature of the anterior end of this rod should be unobscured, and it should be possible to decide whether it is indeed the anterior arm of the tentorium.

The structures labelled "messores" (*mess.*) in fig. 16 have their homologues in the groups described by Anthon, who refers to them as the "pre-mandibles" and suggests that they are modified tormae. He figures them only in part, however, and gives no clear idea of their dorsal connections, so that it is not possible to discuss his interpretation on the basis of his own findings. Reference to the CULICIDAE throws much doubt upon his conception of their nature. Cook points out that in *Chironomus* tormal muscles are present in addition to those of the "pre-mandibles." Following Puri (1925) and Madwar (1937), Cook also points out that the use of the term "pre-mandibles" is unjustified and misleading and himself proposes the term "messor" (*pl. messores*). It should be noted that in his figure of *Theobaldia incidens* the messores articulate dorsally with the internal fold of the paraclypeal phragma, very nearly corresponding to their articulation in *C. nubeculosus*. He derives them from sclerotizations of the lateral wall of the labrum, a derivation which is borne out by their obviously superficial position in Steenberg's (1924) figure of *Phronia* (MYCETOPHILIDAE).

The small sclerotized hooks of the ventral side of the labrum of *C. nubeculosus* articulating with the ventral ends of the messores and carrying the insertions of the labral compressor (figs. 12, 15, and 16, *labr. h.*, fig. 19) do not appear to have any exact homologue in any of the other groups considered. Saunders gives no indication of their presence in *Forcipomyia*, and in *Chironomus*, where there is a labral compressor, the sclerotization on which the muscle is inserted is quite detached from the messores.

It may be noted that the compactness of the mouth region in HELEIDAE

is due to the narrowing of the inter-antennal region. The change in the working plane of the mandibles from horizontal to nearly vertical has been ascribed by Cook to a shift of the anterior mandibular articulations. This is only a partial explanation, for a consideration of the larvae of a number of different families of the Nematocera indicates that the change is also associated with a narrowing of the clypeus in the region of the antennae relatively to its width posteriorly, the inclination of the mandible increasing as the ratio of anterior to posterior width decreases.

6. The Pharyngeal Sclerites.

Sclerotized structures in the region of the anterior end of the pharynx have been described in several Nematoceran larvae; but in none do they reach the complexity found in the CERATOPOGONIDAE, nor is it possible to derive the Ceratopogonid structures from those found in other groups. A well-developed sclerotization of the pharynx occurs in *Delopsis aterrima* (MYCETOPHILIDAE) figured and described by Steenberg (1938); but here, where there are two sclerites, the lateral portions of the posterior one are not articulated, but are immovable projections from the ventral part. The whole structure lies posterior to the opening of the salivary duct without giving off any connections to the labial region, and therefore cannot be regarded as the hypopharynx. In *Chironomus*, Cook (1944b) finds posterior prolongations of the lateral part of the labium, but they do not support any posterior structures as do the obviously homologous struts in *Culicoides*. In other larvae, dorsal complications of the anterior pharyngeal and cibarial regions occur, as in *Phryne*, according to Anthon (1943a), but there is no sclerotization and no lateral linkage with the ventral sclerotization. The pharyngeal complex of CERATOPOGONIDAE, then, has apparently no homologues in other groups, apart from the labial struts of *Chironomus*.

The structures as they occur in *Forcipomyia* (CERATOPOGONIDAE) have been described in detail by Saunders (1924). He recognized that the "hypopharynx" comprised several sclerites besides the one properly so called, but continued to use this term for the whole structure "for convenience." I have used the term in its strict sense for one sclerite and have designated the whole as the "pharynges." Mayer (1934) used "*pharyngeal-skelett*."

There is no difficulty in deciding that the large ventral sclerite is the true hypopharynx. This is established by the presence upon it of the opening of the salivary duct. The position of the frontal ganglion above its posterior edge indicates that this edge marks the position of the morphological mouth.

There seems to be no reason why the heavy, dorsal unpaired sclerite with its attached combs should not be regarded as the epipharynx. At first its position seems to be too far posterior to warrant the use of this term; but if the posterior edge of the hypopharynx marks the position of the morphological mouth, then the dorsal sclerite is still pre-oral and part of the ventral surface of the clypeus. Snodgrass (1935) defines the epipharynx as "a median lobe sometimes present on the posterior (or ventral) surface of the labrum or clypeus." There is no other structure present to which the term could be applied, consequently I have called this sclerite the epipharynx and its posteriorly attached sclerites the epipharyngeal combs.

The lateral arms of the epipharynx are morphologically upside down, for,

in this region, the pre-oral cavity is folded in to form, as it were, a typhosole, and the arms are part of the wall of the "typhosole," i.e., of the upper half of the wall of the cavity. The muscle inserted on the lower mesal face of each arm appears either to be secondarily developed or to belong to a group of cibarial dilators. On the other hand, the muscle inserted on the dorsal end of the arm and directed posteriorly is clearly homologous with the retractor of the mouth angle, for the connective of the frontal ganglion loops over it. Following Snodgrass (1935) the sclerite itself, then, is to be regarded as a dorsal prolongation of the hypopharyngeal suspensorium, lying upside down, the ventral portion having disappeared. In *Forcipomyia* the ventral portion of the suspensorium is still present, and acting as such in linking the hypopharynx with the dorsal end of the lateral arm.

Perhaps the most interesting feature of all the sclerotized structures of the head is the part played by the anterior arm of the tentorium. The messores, the "sub-antennal rings" and the pharynges are obviously special structures, derived from pre-existing elements, though in part grown almost beyond recognition, while the anterior arm of the tentorium, preserving its normal size, integrates the whole, supports the lateral extensions of the cibarium and serves as fulcrum for the epipharynx.

7. The Head Appendages.

i. *The antennae*.—The position of the antennae has already been discussed in the section on the anterior sclerotizations of the head and in the section on antennae in the description of *C. nubeculosus*.

The reduction of the antennae to three segments is common among the larvae of the Nematocera, and even where they are long, as in the CULICIDAE, for instance, the greater length is due to an elongation of one segment.

ii. *The maxillae*.—With the exception of the palpus, which is usually fairly evident, the homologies of the parts of the maxillae in the larvae of Nematocera are often obscure, largely because of the reduction of the whole. In the CULICIDAE and *Chironomus* Cook finds only three distinguishable regions: stipes, palpus and palpifer. Palpifer, of course, does no more than give a name to the region from which the palpus arises. He finds no trace of the cardo.

Stenberg (1938), in describing the Mycetophilid *Delopsis aterrima*, speaks of the palpus, the maxilla proper and the "maxillary plate." This last, which is clearly separated from the body of the maxilla, may be the cardo.

Among the PHRYNEIDAE, TRICHOCERIDAE, LIRIOPEIDAE and PSYCHODIDAE, Anthon describes a maxillary palpus, palpiger, sclerotized cardo and stipes, and lacinia and galea. The lacinia appears to be represented by a membranous cushion, while the galea may be a tubercle or simply an area bearing sensory pegs. In none of these groups, apparently, does the maxilla have an internal skeleton, such as is present in CERATOPOGONIDAE.

iii. *The mandibles*.—The two-segmented character of the mandibles described by Anthon appears to be peculiar to the groups he dealt with and does not occur in *Culicoides*. The rotation of the plane of the mandibles has been discussed by Cook (1949), who, as has already been mentioned, ascribes it entirely to a shift of the mandibular articulations. It has been pointed

out in the section on the anterior sclerotizations of the head that change in the plane of the mandibles is also related to a change in the shape of the clypeus.

iv. *The labium*.—Anthon has shown clearly that the structure present in the larvae of the higher Nematocera often known as the labial plate of submentum is not part of the labium at all. His diagrams of the series PHRYNIDAE, TRICHO CERIDAE, PSYCHODIDAE and LIRIOPEIDAE show that the labium itself has been withdrawn into the pre-oral cavity and that the "labial plate" is a development of the "hypostomal bridge." The situation is not at all obvious when the labium is much reduced and may be realized only on section, when it becomes apparent, as in *C. nubeculosus* (fig. 10).

SUMMARY.

The egg, some aspects of the late embryo, the four larval instars and the pupa of the biting midge *Culicoides nubeculosus*, taken originally in Dorset, are described. Attention is called to the presence, in the first instar only, of a reduced prothoracic pseudopod, and to its resemblance to that found in the genus *Apelma*, of the same family, the CERATOPOGONIDAE, where it is present throughout larval life. The anatomy of the fourth instar larva is considered in detail, and its chaetotaxy is related to that of the larva of *Forcipomyia*, also of the same family, as described by Saunders (1924). Descriptions by Cook (1944), Anthon (1943a) and Steenberg (1924-5, 1938) of other nematoceran larvae are considered, and from them it is attempted to derive the morphology in *C. nubeculosus* of the sclerites of the head capsule, the accessory sclerotizations in the region of the functional mouth and of the complex skeleton surrounding the anterior end of the pharynx commonly known as the "hypopharynx," which appears to be peculiar to the CERATOPOGONIDAE.

It is shown that the dorsal median sclerite of the head capsule is the fronto-clypeus, and that the sclerite forming the rest of the capsule is made up of the post-genae and forward extensions of the post-occiput. The so-called labium is shown to be formed from a forward extension of the sub-genal ridges which have met and fused in the mid-ventral line; while the true labium is much reduced and has been withdrawn into the functional mouth. The sclerotizations of the labrum are shown to be equivalent to the messores of the CULICIDAE, described by Cook (1944). The internal sclerotizations of the head are shown to be in part a complex formed from the anterior end of the tentorium, while the others are true hypopharynx and a complex epipharynx. Thus there is a pre-oral cavity or cibarium of considerable size, the morphological mouth having been withdrawn to a position near the middle of the head.

The detailed structure of the epipharynx appears to be reasonably constant within the species, but an exception is noted among the Dorset specimens and other differences are found in a Scottish form. The suggestion may be made that the species is not homogeneous.

There are only two Malpighian tubes, unlike the terrestrial larvae of *Forcipomyia*, where there are three.

In the pupa the number of spiracular endings, the papillae, of the prothoracic respiratory horn varies within narrow limits, so that the separation of closely allied species may be difficult on this character alone. The degree

and extent of the pigmentation of the horn, however, appears to be fairly constant in the Dorset specimens, but differences in this respect are noted in Scottish forms, thus further indicating heterogeneity. In this connection the absence of pigment spots from the abdomen is a noteworthy difference from the *C. nubeculosus* described by Mayer (1943a).

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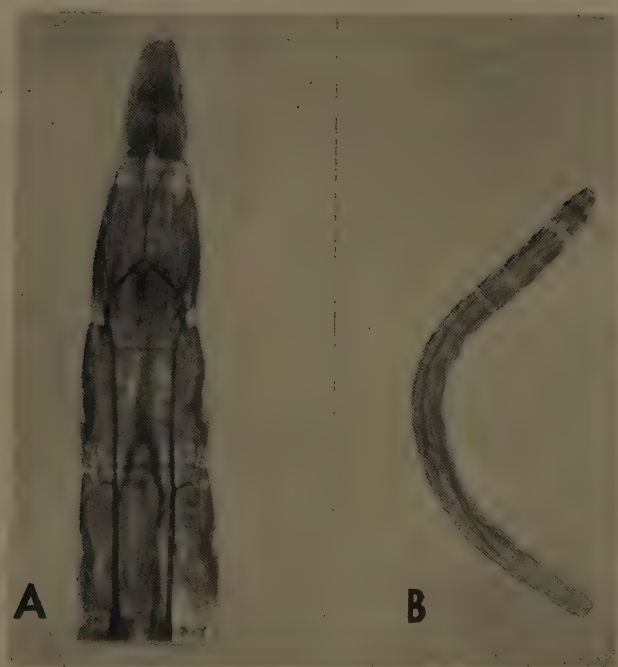
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A. Dorsal view of head and thorax of 4th instar larva of *Culicoides nubeculosus*. $\times 55$.

B. Dorsal view of newly hatched 1st instar larva. $\times 55$.

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ERRATA.

- P. 180, line 12, for "*Haliperus*" read "*Halipeurus*."
P. 185, line 12, for "*Haliperus*" read "*Halipeurus*."
P. 224, line 30, for "*pretosa*" read "*pretiosa*."

